Resource selection by the brushtail possum (*Trichosurus vulpecula* Kerr) in a mixed red - silver beech (*Nothofagus fusca* - *N. menziesii*) forest, north Westland, New Zealand: a multi-scale, GIS-based approach.

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Abstract

Resource selection by the brushtail possum (*Trichosurus vulpecula*) was studied in a beech (*Nothofagus*) forest in order to elucidate possum ecology in an extensive forest type lacking extensive possum research. The study was conducted in the Upper Grey Valley, north Westland, on a post-glacial terrace dominated by *Nothofagus fusca* and *Nothofagus menziesii* and dissected by a gravel road.

Five principal research questions were posed for the study of possums within the site. These were:

1. What are the movement parameters of the resident possum population?
2. What are the patterns of vegetation heterogeneity?
3. What constitutes possum diet?
4. What are the relationships between possum diet and vegetation heterogeneity?
5. What are the relationships between possum movements and vegetation heterogeneity?

Twelve possums were radio-collared and radio-tracked over a year. Home ranges calculated with the kernel method averaged 8.1 ± 1.0 ha (mean ± s.e.), which is large when compared to possum home ranges observed in other continuously forested sites. Range lengths were similarly large (456 ± 42 m). Bi-monthly variation was only displayed with significantly smaller home ranges in winter when compared to autumn.

Despite the fact that the study site was generally dominated by *N. fusca* and *N. menziesii*, considerable heterogeneity existed with respect to the possum palatable species within the site. Many palatable species such as *Aristotelia serrata*, *Fuchsia excorticata*, *Muehlenbeckia australis* and *Trifolium repens* occurred predominately along the roadside, whilst *Weinmannia racemosa* occurred predominately on steep areas within the forest. TWINSPAN classification of the forest identified three vegetation communities. These were open sites, including the road and swamp areas, steep areas, including the hill and escarpments, and terrace areas.

Resource selection by possums within the site was investigated with diet preference analysis, habitat selection analysis and modelling of use of space versus resource variables. Diet preference was analysed by comparing the level of consumption of food types with their level of availability within the site at multiple scales. The top five ranked preferred food types, calculated overall, were, in decreasing rank, *Fuchsia excorticata* foliage, *Carpodetus serratus* fruit, *Rubus cissoides* foliage, *Muehlenbeckia australis* foliage and *Pseudopanax colensoi* fruit.

Habitat selection analysis indicated that although overall selection was not occurring, possums exhibited a degree of preference towards the terrace community. Modelling of resource variables against use of space indicated that although there was latent variability between individual possums, there was a trend for greater use of areas with high abundance of preferred species. Modelling of pooled possum use of space on an annual scale indicated that use was positively correlated with species richness and negatively correlated with *N. fusca*, *Quintinia acutifolia*, and *Coprosma rotundifolia* abundance, which are all unpreferred species. Annual home ranges of possums were found to be negatively correlated with forage quality as defined by preferred species.

A model of possum resource selection within the site was postulated to the effect that possums choose their home range location randomly, with respect to vegetation heterogeneity, and then modify the size of their home range to suit nutritional needs rather than modifying range location.

The ranging behaviour and resource selection of possums observed in this study have implications for the management of possums in similar forest types. Efficiency of control and monitoring operations may be increased by using a spacing regime derived from possum home ranges. Inferences obtained from habitat selection analysis indicate that stratification of control and monitoring operations is not warranted in similar forest types. The development of extensive models with predictive capabilities for the distribution of possums within the environment has the ability to become a useful tool for possum managers. Further research of potential benefit could include investigation into resource quality and availability, the effect of home range size on residual trap catch (RTC) indices, improving diet assessment techniques and assessing possum preference for non-foliar food types.

Chapter 1: Introduction

The purpose of this chapter is to provide context to and justification for the research undertaken in this study. This is achieved by outlining the unique evolution of New Zealand's flora and fauna, and its inherent vulnerability to introduced mammals. Following this, New Zealand's conservation mindset is discussed in relation to controlling legislation. The subject of this thesis, the brushtail possum (*Trichosurus vulpecula* Kerr, 1792), is introduced with a description of the species and the major issues surrounding its management. Justification for the specific research topic is then given and is followed by an outline of the thesis.

1.1 New Zealand's uniqueness and vulnerability

The indigenous flora and fauna of New Zealand has evolved through a long history of isolation from other land masses. New Zealand separated from the Gondwana super-continent in the late Cretaceous 60-80 million years ago, and, as such, was somewhat isolated from the proliferation of mammals and flowering plants that occurred in the tertiary era (Stevens, 1980). Consequently, much of New Zealand's flora and fauna is endemic (Bull and Whitaker, 1975; Wardle, 1991). Of particular interest is the lack of indigenous terrestrial mammals, excepting three bat species (Atkinson, 2001). Because indigenous flora and fauna has not had the opportunity to evolve specific attributes to coexist with such species, introduced mammal species pose a serious threat to New Zealand's natural ecosystems (Salmon, 1975; Wodzicki and Wright, 1984).

The list of mammals introduced into New Zealand is lengthy, but not all of them have become established or have achieved pest status (Wodzicki and Wright, 1984; McDowell, 1994). Thirty two mammal species have become established including rabbit, hare, six species of wallaby, mouse, three species of rat, cat, weasel, stoat, ferret, hedgehog, feral goat, feral sheep, feral pig, feral horse, feral cattle, chamois, thar, seven species of deer and brushtail possum (Wodzicki and Wright, 1984). The

impacts of the most problematic species on indigenous systems are summarised from Atkinson (2001) as follows:

- Rabbits and hares typically graze grasslands, but may also have an impact on the regeneration of shrubs and trees;
- Rats, cats, weasels, stoats and ferrets are predators of indigenous invertebrates, amphibians, lizards and birds;
- Goats, sheep, horses, cattle, chamois, thar and deer browse forests, scrub grasslands and alpine herbfields, and prevent the regeneration of many species of palatable plant;
- Hedgehogs and pigs are omnivores and their impacts are poorly understood;
- Possums have the ability to alter forest composition through selective browsing of the forest canopy and other forest components.

Most of these species represent a threat to biodiversity, but the most serious threat is posed by the brushtail possum (Salmon, 1975; Atkinson, 2001).

1.2 Conservation mindset

Since the first European importations of mammals into New Zealand in 1773 (Thomson, 1922), considerable resources have been aimed at control of these species, yet for different reasons at different times. Ironically, some of the first instances of control of introduced mammals were undertaken to promote the establishment of other introduced species (McDowell, 1994), but more commonly control was aimed at the reduction of 'nuisance' populations of introduced mammals (Salmon, 1975). Early protections were placed on some of the more valuable species, but these were eventually lifted in favour of harvesting for economic value or sport (Thomson, 1922).

In 1907 legislation was passed conferring protection to specific indigenous flora and fauna, and was followed by the Animals and Game Protection Act 1921, which broadened the spectrum of protected indigenous species, but also protected some introduced species such as the possum (Salmon, 1975). It is likely that such legislation reflected an increased awareness of the value of indigenous flora and fauna. By 1930, widespread damage to New Zealand's natural landscapes caused by

introduced mammals had become evident and remaining protection of such animals was lifted in favour of large-scale culling operations (Salmon, 1975).

Initially, control was aimed at ameliorating the impact of mammal species on hydrological processes, such as erosion and sedimentation, but in the late 1970s there was a paradigm shift towards protection of intrinsic conservation values, providing a concomitant protection of hydrological processes (Holloway, 1993). More recent strategies in the control of introduced mammals include the eradication of species from offshore islands (e.g. Taylor and Thomas, 1993; Veitch, 2001), the creation of intensively controlled 'mainland islands' (Saunders and Norton, 2001), and the development of integrated pest management strategies (Coleman, 1993), which sometimes includes the previous two strategies. Considerable interest is currently being invested in developing biological control methods for some species, especially possums, as this has the potential to provide self-sustaining control without the drawbacks of conventional control methods, such as use of poisons (Cowan, 2000a).

Introduced mammals may be classified under two main pieces of legislation. The Wild Animal Control Act 1977 defines most ungulates and marsupials as pests, and the Wildlife Act 1953 classifies rodents, mustelids, feral cats and hedgehogs as unprotected animals under schedule six. Animals that are not specifically classified can be included in regional pest management strategies, drafted under the Biosecurity Act 1993. Current pest control is usually undertaken under the Conservation Act 1987 for central government, or under the Resource Management Act 1991 and the Biosecurity Act 1993 for regional government.

1.3 Possum background

1.3.1 Liberations and distribution

Brushtail possums were first introduced into New Zealand in the late 1830s for the purpose of establishing a fur industry (Pracy, 1974). Between 1837 and 1960, a total of 464 declared liberations were made throughout the country and with the advent of the Department of Internal Affairs bounty system in 1950 many more undeclared liberations were made from New Zealand bred possums (Pracy, 1974). Further

private liberations have been made more recently into areas previously unoccupied, such as Northland (Clout and Ericksen, 2000).

Possums are now distributed throughout the three main islands of New Zealand, but are absent from the western-most parts of Fiordland as well as from several offshore islands (Clout and Ericksen, 2000). It has been estimated that they are extant in over 95% of New Zealand's land area (Parkes *et al.*, 1997; PCE, 2000).

1.3.2 Biology

Brushtail possums in Australia have the most widespread native distribution of any Australian marsupial and are found in almost all but the wettest forested areas (Kerle, 1984). The ability to utilise such a diverse range of habitats has been attributed to the plasticity of its morphology, behaviour and diet (Kerle, 1984). In New Zealand, possums have successfully colonised almost every habitat available; they can be found in tussock grassland, temperate rainforests, sand dunes, montane scrublands, farms, urban areas and exotic forests (Green, 1984). It appears that the only specific habitat requirements for possums in New Zealand are vegetation and shelter.

Possums in New Zealand typically weigh between two and three kilograms and exhibit a north-south cline in body weight, as weight increases with increasing latitude (Cowan, 1990a). Generally there are two colour forms, grey and black, however, browns and reds of varying degrees also occur and are likely to be mixtures of the true-breeding grey and black forms (Cowan, 1990a). Congruent with the dichotomy in Australian brushtail possums, black colour forms tend to dominate in the wetter areas of New Zealand (Brockie, 1992).

Possums are nocturnal and are typically active outside of their dens from about 30 minutes after sunset to just before dawn in summer and often several hours before dawn in winter (Ward, 1978; MacLennan, 1984). A study in an open eucalypt forest in Australia indicated that possums spend 16 % of their total time out of their dens feeding, 30 % travelling, ten percent grooming, one percent interacting and 43 % inactive (MacLennan, 1984). It has been postulated that long periods of inactivity are an energy conservation measure adopted in response to an energy balance problem

concerning the high toxin content of their predominately *Eucalyptus* diet (MacLennan, 1984).

However, their behaviour in New Zealand is likely to be different from that in Australia for three reasons:

- Possum diet in New Zealand primarily consists of species that contain low toxin levels (Fitzgerald, 1978; Brockie, 1992);
- There is a greater abundance and availability of palatable species in New Zealand, as they have evolved in the absence of mammalian herbivores (Fitzgerald, 1984);
- Predation on possums in New Zealand is relatively low (Clout and Ericksen, 2000).

For these reasons, it could be assumed that the low toxin diet of possums in New Zealand would lead to less need for inactivity to combat the metabolic cost of processing toxins. The increased food availability would be likely to lead to decreased feeding activity by increasing feeding efficiency and the absence of terrestrial predators could be expected to prompt more terrestrial activity.

Reproductive maturity for both sexes usually occurs after one to two years, however reproductive success for females is low for the first year or two of maturity (Cowan, 1990a; Fletcher and Selwood, 2000). Births are most common in autumn, but occasionally a spring pulse of births occurs as a result of early breeding in the previous autumn or double-breeding which is thought to be associated with abundant food sources (Kerle, 1984; Cowan, 1990a; Fletcher and Selwood, 2000).

Typically, possums disperse from their natal area after roughly a year spent with their mother (Clout and Efford, 1984; Ward, 1985; Cowan *et al.*, 1996; Cowan *et al.*, 1997a). Males disperse several kilometres and appear to disperse furthest across agricultural landscapes, whereas females tend to settle near their natal area (Clout and Efford, 1984; Ward, 1985; Cowan *et al.*, 1996; Cowan *et al.*, 1997a). It is thought that factors such as competition for food, den sites and mates influence the decision to settle after dispersion (Cowan, 2000b). Other factors may include the distance travelled and the number of attempts made to settle, but this process has not been specifically addressed in the literature.

Once settled, possums generally become sedentary and form stable home ranges (Crawley, 1973; Jolly, 1976; Ward, 1978; Brockie *et al.*, 1989). Males tend to have larger annual home ranges than females, which is thought to be related to their heavier body weight (Green, 1984), but could also be related to breeding behaviour (Ward, 1978). Although possum dominance hierarchies do exist in the wild (Jolly, 1976) and in captivity (Spurr and Jolly, 1999), territorial behaviour in New Zealand is rare and consequently there is considerable overlap between individual's home ranges (Crawley, 1973; Jolly, 1976; Ward, 1978; Green and Coleman, 1986).

1.3.3 Diet

Foliage comprises the bulk of possum diet (Statham, 1984; Cowan, 1990a), which differs from region to region within New Zealand (e.g. Harvie, 1973; Coleman *et al.*, 1985; Owen and Norton, 1995; Allen *et al.*, 1997; Cochrane and Norton, 2000; Cochrane *et al.*, 2003; Sweetapple, 2003). However, a common theme in all regions is the tendency for the bulk of the diet to consist of a few species (Fitzgerald, 1976; Fitzgerald, 1978; Warburton, 1978; Fitzgerald and Wardle, 1979; Fitzgerald, 1984; Owen and Norton, 1995; Cochrane *et al.*, 2003). Choice of diet is influenced by relative preference and availability of food types, as well as specific nutritional requirements (Fitzgerald, 1976). Preferred species are generally those with the lowest chemical defences and highest energy and nutrient content (Fitzgerald, 1976; Fitzgerald, 1978). Typically, these are fast-growing seral and liane species such as *Aristotelia serrata*[1], *Fuchsia excorticata* and *Muehlenbeckia australis*, but also include relatively fast-growing subcanopy and canopy species such as *Weinmannia racemosa*, *Metrosideros umbellata, Metrosideros robusta* and *Beilschmiedia tawa.*

Flowers and fruit are a seasonally important food source for many possum populations (Fitzgerald, 1976; Cowan, 1990b; Owen and Norton, 1995; Cochrane *et al.*, 2003). It is likely that fruits and flowers are an underestimated constituent of possum diet when assessed using standard techniques due to their high digestibility

[1] Plant nomenclature follows Allan (1961), Moore and Edgar (1970), Connor and Edgar (1987), Webb *et al.* (1988), Brownsey and Smith-Dodsworth (1989), Mitchell *et al.* (1997), and Edgar and Connor (2000).

relative to foliage (Cowan, 1990b). The attractiveness of fruit is likely related to its seasonally high abundance and its high net energy returns (Williams, 1982; Cowan, 1990b).

Although possums are thought of as primarily herbivorous, recent studies have indicated that non-plant food types, such as invertebrates and fungi, are an important part of possum diet. Many possum diet studies conducted in New Zealand have detected invertebrate consumption, with a positive relationship between consumption and invertebrate abundance and activity being postulated (Cowan and Moeed, 1987). Seasonal consumption of fungi also occurs and, as with fruit, is likely to be underestimated in the diet due to its high digestibility relative to foliage (Cochrane *et al.*, 2003). Possums have also been observed to prey on birds, birds' eggs and small mammals, both alive and dead (Brown *et al.*, 1993). However, the frequency and importance of such events is poorly understood.

1.3.4 Impacts

Possums have two differing types of negative impact on New Zealand's environment: the first is related to their diet, the second is related to their spread of infectious organisms.

1.3.4.1 Diet related impacts

Concerns over possums' impact on native vegetation surfaced around the 1920s but were largely dispelled by scientists such as Professor H. B. Kirk and Dr L. Cockayne, as they insisted that possum impacts were negligible and in any case would be outweighed by the financial benefits they provided (Pracy, 1974). Today, possums are recognised as one of the most serious threats to New Zealand's natural ecosystems because of their ability to drastically alter forest composition (Salmon, 1975; Wodzicki and Wright, 1984; Peterson *et al.*, 1994; Nugent *et al.*, 2001).

Because possum feeding behaviour is selective, preferred species are consumed in greater amounts than their abundance would predict (Gilmore, 1967; Fitzgerald, 1976; Fitzgerald, 1978; Fitzgerald and Wardle, 1979; Coleman *et al.*, 1980; Fitzgerald,

1984; MacLennan, 1984; Owen and Norton, 1995; Pekelharing *et al.*, 1998a; Cochrane *et al.*, 2003). This behaviour leads to preferred species being targeted until they are rare or locally extinct (Fitzgerald, 1976). Selective behaviour also extends to the level of individual trees of the same species (Jolly, 1976; Meads, 1976; MacLennan, 1984). In many cases, individual trees are the subjects of repeated defoliation while neighbouring trees of the same species are left relatively untouched. Selective browsing of individual trees over consecutive nights makes it very difficult for them to recover and frequently results in mortality. It is this ability to induce localised mortality that enables possums to alter forest composition so drastically.

New Zealand's primary production landscapes do not escape impact from possums. Production forestry can suffer from damage to young trees and seedlings (Warburton, 1978; Jacometti *et al.*, 1997), and agricultural and horticultural areas can suffer from locally significant losses in productivity due to grass and crop consumption by possums (Peterson *et al.*, 1994; Butcher, 2000).

1.3.4.2 Spread of infectious organisms

Possums are known vectors of several diseases that pose a serious threat to the dairy, beef and venison industries (Animal Health Board, 2000), and to the quality of waterways (Peterson *et al.*, 1994).

Possums were first implicated as vectors of bovine tuberculosis (Tb) in the late 1960s and early 1970s when Tb infected possums were found coexisting with chronically infected cattle herds (Coleman and Caley, 2000). This discovery has lead to significant possum control in forested areas adjoining cattle or deer farms with the aim of reducing possum numbers below the critical levels of Tb maintenance within possum populations. Control effort is planned to be significantly increased in rural areas in the next decade in an ambitious attempt to effectively eradicate Tb from livestock herds (Animal Health Board, 2000).

Tourism in New Zealand may suffer indirectly from possums due to their implication in the spread of water-contaminating micro-organisms such as *Giardia* and *Cryptosporidium* (Peterson *et al.*, 1994). Contaminated waterways in our national

parks may severely tarnish New Zealand's 'clean, green' image, on which it relies heavily for tourism.

1.3.5 Possum control

It wasn't until the 1940s that the Department of Internal Affairs recognised the destructive nature of the drastically increasing possum population by lifting all restrictions on the harvesting of possums, and initiating a bounty scheme (Pracy, 1974). While this resulted in a considerable number of possums being killed, the control effort was without direction; consequently, most control effort centred on 'easy' populations close to developed areas (Parkes *et al.*, 1997). As such the bounty scheme was ceased in 1961 (Peterson *et al.*, 1994) and aerial sowing of baits containing sodium monofluoroacetate (1080) developed into a major method for the control of possums in more inaccessible regions (Parkes *et al.*, 1997).

1.3.5.1 Toxin use

Toxins currently used for possum control include cyanide (Feratox® and pastes), 1080, cholecalciferol (Campaign®), phosphorus paste, brodifacoum (Talon® and Pestoff®) and pindone (Eason *et al.*, 2000). All can be used for ground-based control, but 1080 has proved to be the most suitable for use as an aerially applied control measure (Peterson *et al.*, 1994).

Aerial application of baits containing 1080 was first adopted by the New Zealand Forest Service in 1956 (Morgan *et al.*, 1996; Morgan and Hickling, 2000), and is continued today by the Department of Conservation (DOC) and regional councils, themselves, and as agents of the Animal Health Board (DOC, 1994; Peterson *et al.*, 1994; Parkes *et al.*, 1997; Animal Health Board, 2000; Clout and Ericksen, 2000). Aerial application of 1080 is currently the preferred method for the initial control of possum populations in rugged or remote terrain because it frequently delivers kill rates better than 80 % and large areas can be covered in short periods of time (Morgan *et al.*, 1996; Warburton, 1996; Morgan and Hickling, 2000).

Despite the apparent success of aerial application of 1080 in control operations, there is much concern over the secondary impacts it has on the environment. Although 1080 has been shown to degrade quickly and harmlessly in the environment (DOC, 1994; Meenken and Eason, 1995; Beasley, 1996; Eason *et al.*, 2000), many people still believe that residual effects on waterways, fauna and soils have occurred. 1080 can remain in high concentrations in the remains of poisoned animals and any animals feeding on such carrion are likely to suffer secondary poisoning, to which dogs are especially susceptible (DOC, 1994; Beasley, 1996; Eason *et al.*, 2000). However, this effect can be beneficial, as 1080 application for possum control can also provide significant control of introduced predators.

Historically, the aerial application of 1080 suffered from poor planning and implementation. Often poison would be dropped outside of the intended areas and the actual baits themselves were not designed to discourage consumption by indigenous fauna (Peterson *et al.*, 1994; Morgan and Hickling, 2000). Considerable advances have been made in both the accuracy of poison application (e.g. through the use of GPS technology) and the treatment of baits to make them unattractive to non-target animals (DOC, 1994; Peterson *et al.*, 1994; Morgan *et al.*, 1996). This has had the effect of reducing overall toxin input into the environment as well as reducing the impact of toxins on indigenous fauna.

In easily accessed or sensitive areas, such as farmland, lands commonly used by local communities and areas that require sustained control, ground-based control techniques are preferred over aerial methods. This is primarily because operators have more control over bait locations and can, therefore, minimise the risk of undesirable exposure to people or animals (Morgan and Hickling, 2000).

It appears that the public cannot reach consensus as to whether the damage caused by possums justifies the introduction of toxins into the environment. It is likely that public opinion is influenced by historically 'safe' toxins proven 'unsafe' such as DDT, PCBs, PCP and Agent Orange (Peterson *et al.*, 1994). The connotations associated with using pesticides in natural environments are powerful and are difficult to resolve, consequently, the use of poisons in the environment is likely to remain a point of contention.

1.3.5.2 Biocontrol

In light of the concerns surrounding toxin use for pest control, biocontrol has been suggested as a primary control alternative. Biocontrol is seen as a powerful tool that can be used in conjunction with standard control techniques in an integrated pest management strategy. Such an approach has the potential to achieve pest control goals in a long-term cost-effective way (Cowan, 2000a).

Potential biocontrol mechanisms of possums in New Zealand have been the focus of much recent research (RSNZ, 1998). Promising research directions include parasites and diseases, as well as physiological controls such as fertilisation, embryonic development, post-natal development, central endocrine control of reproduction, passive immunity and lactation (Cowan, 2000a). Considerable advances are also being made in the development of delivery systems for these biocontrol agents (Cowan, 2000a).

1.4 Justification for study

Historically, studies on the possum in New Zealand have been focused on forests with high diversity and palatable canopies. The reason for this is twofold; possum density in these forests is generally high (Efford, 2000), and forest damage is readily apparent (e.g. Batcheler, 1983). Consequently, *Nothofagus* forest has been largely overlooked because possum densities within these forests are generally low (Efford, 2000), its canopy is generally unpreferred (James, 1974), the overall level of extant biodiversity is low (Owen and Norton, 1995; Cochrane *et al.*, 2003), and indicators of possum impact are likely to be subtle. This tendency is reflected in the literature with only a handful of studies having been focused on possums in *Nothofagus* or mixed *Nothofagus* / broadleaved angiosperm forest. Most of these are listed and described as follows:

Clout and Gaze (1984) examined a possum population in a mixed *N. fusca* / *N. menziesii* forest at Mt. Misery in the Nelson Lakes National Park. The study investigated many aspects of the population including structure, breeding success,

movement, and density change with altitude. Movements of individuals were determined by live trapping, which yielded estimates of range sizes but gave no real indication of habitat utilisation.

Rose *et al.* (1993) estimated the impact of invading possums in South Westland *Nothofagus* / broadleaved forests. The focus of their study was on conspicuous canopy mortality of *Metrosideros umbellata* and *Fuchsia excorticata* induced by possum browse. They observed strong correlations between length of possum occupation and canopy dieback, and commented that possum impact reflected the abundance of possum-preferred canopy species.

Norton and Owen (1995) investigated the link between the diet of possums and the abundance of palatable species in *N. menziesii* forest in South Westland. They found that only a few species made up the bulk of the diet, such as *A. serrata* and *M. australis*, which indicated that possum were feeding in a non-random fashion.

Pekelharing *et al.* (1998a) conducted a study in a mixed *N. fusca* / *N. menziesii* forest at Springs Junction, north Westland, and investigated the seasonal patterns of possum browse on five possum-preferred species; *Raukaua simplex*, *Pseudopanax colensoi*, *A. serrata*, *Elaeocarpus hookerianus* and *P. crassifolius*. Browse was shown to be markedly seasonal, with the most severe browse occurring in winter/spring. The two most heavily browsed species were *R. simplex* and *P. colensoi*, and it was these species that suffered the greatest mortality.

Pekelharing *et al.* (1998b) studied the effect of possum browse on growth of *Fuchsia excorticata* at five sites in south Westland dominated by *Nothofagus* species. Browse was significantly positively related to the density of possums at each site. Tree mortality was observed to occur after two years if possums were not controlled, but the impact of possums was halted and reversed with timely control.

Sweetapple (2003) investigated the diet of possums in a forest sequence comprising mixed *N. fusca* / *N. menziesii* forest in lower areas grading into *N. solandri* var. *cliffortioidies* forest in upper areas. High consumption of *Nothofagus* seed and moderate consumption of *Nothofagus* foliage was observed in a mast year and high

consumption of *Nothofagus* foliage was observed in a non-mast year. Fungi were also found to be an abnormally high component of the diet at this site. It was postulated that the low abundance of typical possum preferred species within the site lead to possums making more extensive use of alternative food sources.

Cochrane *et al.* (2003) assessed the diet of a possum population in a mixed *N. fusca* / *N. menziesii* forest, north Westland. As with Norton and Owen (1995), they found that only a few species made up the bulk of the diet. The abundance of the various palatable species was assessed in several broad vegetation types in order to gain an indication of preference. It was found that seral, liane and understory species such as *A. serrata*, *M. australis* and *W. racemosa* were utilised by possums disproportionately to their abundance in the forest, indicating non-random selection. A strong variation in diet over different seasons was also observed as possums made use of seasonally abundant flowers and fruit.

These studies indicate that possums have little impact on *Nothofagus* species themselves (*but see* Sweetapple, 2003) but make extensive use of understory and seral species, often leading to mortality of these latter species. As such, the influence of possum browse within *Nothofagus* forest is unlikely to result in significant canopy dieback, as has been observed in other forest types (e.g. Campbell, 1990; Rose *et al.*, 1993). Nevertheless, possums have the potential to adversely affect the biodiversity of these species-poor *Nothofagus* systems because the species consumed by possums comprise a disproportionately large part of such biodiversity (Owen and Norton, 1995; Cochrane *et al.*, 2003).

When it is considered that possum-preferred species within *Nothofagus* forest provide a large proportion of fruit and flowers available to indigenous birds and insects (Wardle, 1984), any loss of these species would have serious implications for the wider ecosystem due to deterioration of pollinator / disperser mechanisms. In other more complex forests there is unlikely to be such a high dependency on so few species, and, therefore, such forests could be expected to be more ecologically resistant to possum impacts.

These observations contrast with previous views that possum impacts within *Nothofagus* forest were likely to be low (e.g. Wardle, 1974; Peterson *et al.*, 1994). Given the small amount of investigation into possum ecology within *Nothofagus* forest and the fact that *Nothofagus* forest is the most abundant forest type in New Zealand (Wardle, 1991), there is an obvious need for further possum research in this forest type.

Although research of possum diet is likely to provide the greatest insights into their impacts, it is also important to understand how possums utilise their environment spatiotemporally. Knowledge of what possums eat in specific forest types may provide insights into *what* impacts are likely to occur, yet knowledge of spatiotemporal utilisation may provide insights into *where* such impacts are likely to occur. Furthermore, knowledge of spatiotemporal variation in utilisation may lead to greater efficiencies in control and monitoring. Such knowledge may be attained with resource selection analysis.

Mounting environmental concerns over poison use in the environment has prompted considerable effort towards improving the efficiency of poisoning operations, with the general goal of reducing the amount of toxins introduced into the environment whilst retaining or improving kill rates (Innes and Barker, 1999). Resource selection analysis may identify preferences for areas or attributes of areas, which could then be used to improve the efficiency of control and monitoring by promoting stratified operations.

Presently, the residual trap catch (RTC) method is the primary monitoring approach for the Department of Conservation (DOC), regional councils and researchers (Warburton, 2000). In an effort to standardise the technique, protocols have been drafted by the National Possum Control Agency (NPCA) (2000). They advocate a stratified approach whereby trapping lines are allocated into strata of differing possum densities; (NPCA, 2000) an equivalent approach would be to stratify by activity. However, stratification by intuition is potentially dangerous, as key areas may be missed. Habitat selection analysis offers a much more robust method of determining appropriate strata by describing the spatial habitat utilisation patterns and ordering habitats by preference.

Given the potential for disruption of ecosystem processes with *Nothofagus* forests and the potential for resource selection analysis to better understand the utilisation of such forests by possums, an investigation of possum resource selection in *Nothofagus* forest is warranted.

1.5 Research outline

This thesis addresses five fundamental questions relating to possum resource selection within the study site. These are outlined as follows:

1. What are the movement parameters of the resident possum population?
2. What are the patterns of vegetation heterogeneity?
3. What constitutes possum diet?
4. What are the relationships between possum diet and vegetation heterogeneity?
5. What are the relationships between possum movements and vegetation heterogeneity?

The main body of this thesis comprises five further chapters; the first is descriptive, the following three are research based and the fifth is a final concluding chapter. These are outlined as follows:

- **Chapter 2: Study site**
  The research site chosen for this study is described in terms of location, climate, topography/physiography, geology/lithology, general vegetation and possum history. The purpose of this chapter is to describe the general conditions in which the studied possum population lived.

- **Chapter 3: Possum movements**
  This chapter describes and analyses the ranging behaviour of radio-tracked possums in order to elucidate the spatiotemporal movement parameters of the resident possum population. These movement parameters are then discussed in context with other studies of possum movements.

- **Chapter 4: Vegetation heterogeneity**

  Within this chapter species distributions are given, the phenology of common possum-preferred species is described, vegetation communities are classified and the vegetation within the site is discussed in context with other *Nothofagus* forests that have been subject to possum research.

- **Chapter 5: Resource selection**

  There are three main components to this chapter and all utilise components of the previous two chapters. Possum diet within the site is examined and analysed for preference using the species distributions derived in the vegetation heterogeneity chapter. Habitat selection is conducted with compositional analysis using the home ranges defined in the possum movements chapter and the vegetation communities defined in the vegetation heterogeneity chapter. Modelling of possum use of space versus multiple resource variables similarly utilises information from the previous two chapters.

- **Chapter 6: Final conclusions**

  This chapter places the findings of each chapter into context with each other and with research conducted elsewhere in order to develop a descriptive model of possum resource use within the study site and to provide management implications. The thesis is concluded with suggestions for potential areas of research.

Chapter 2: Study Area

2.1 Location

The study site where research was undertaken was located approximately 15 km southwest of Springs Junction, north Westland, New Zealand (42°27'S, 172°04'E), in terrace *Nothofagus* forest above the Upper Grey River (Figure 2.1). The site was accessed by Palmer Road, which turns off State Highway 7, four kilometres to the west of Springs Junction. Boundaries of the study site were marked by Hawker Creek to the south, the base of Slate Slip Hill to the southeast, the Upper Grey River to the northwest and the second unnamed creek to the north of Hawker Creek (Figure 2.2). Altitude varied from 360 m a.s.l. to 640 m a.s.l. and the approximate area of the study site is 120 ha.

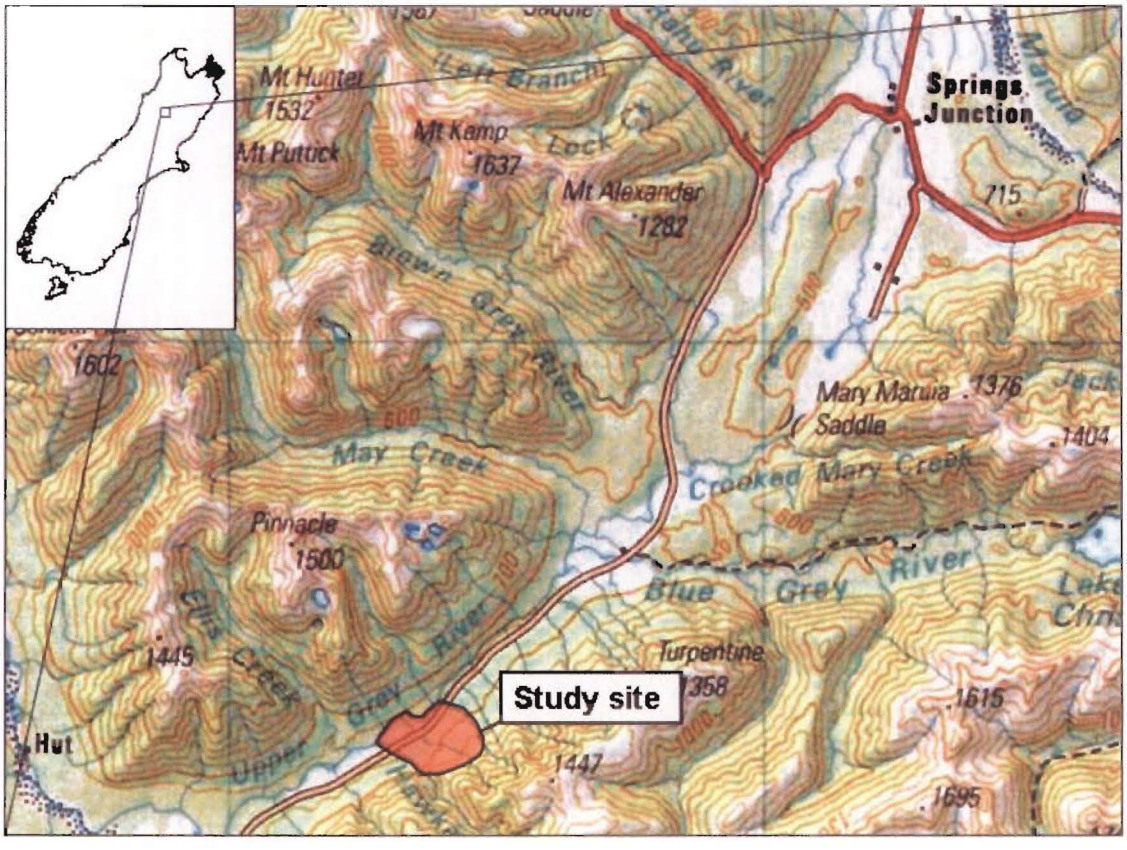

Figure 2.1: Study site location.

2.2 Topography / physiography

The site was located on a northwest facing post-glacial terrace primarily formed by the Upper Grey River. Upper areas of the terrace were moderately sloped (10-20°), whilst the lower areas were near flat (2-6°). The terrace was intersected by a series of streams that were steep and heavily incised in the upper sections, but flowed more gently through the middle and lower sections. Apart from the upper stream areas, the only other steep areas in the study site were the base of Slate Slip Hill, which had a slope frequently in excess of 40°, and the escarpments, which were found above the northern half of the roadside and below the southernmost third of the roadside. Seepage from the main terrace had lead to the formation of open swamps below the southern half of the road, immediately above the Upper Grey River, which covered an area of approximately 2.5 ha.

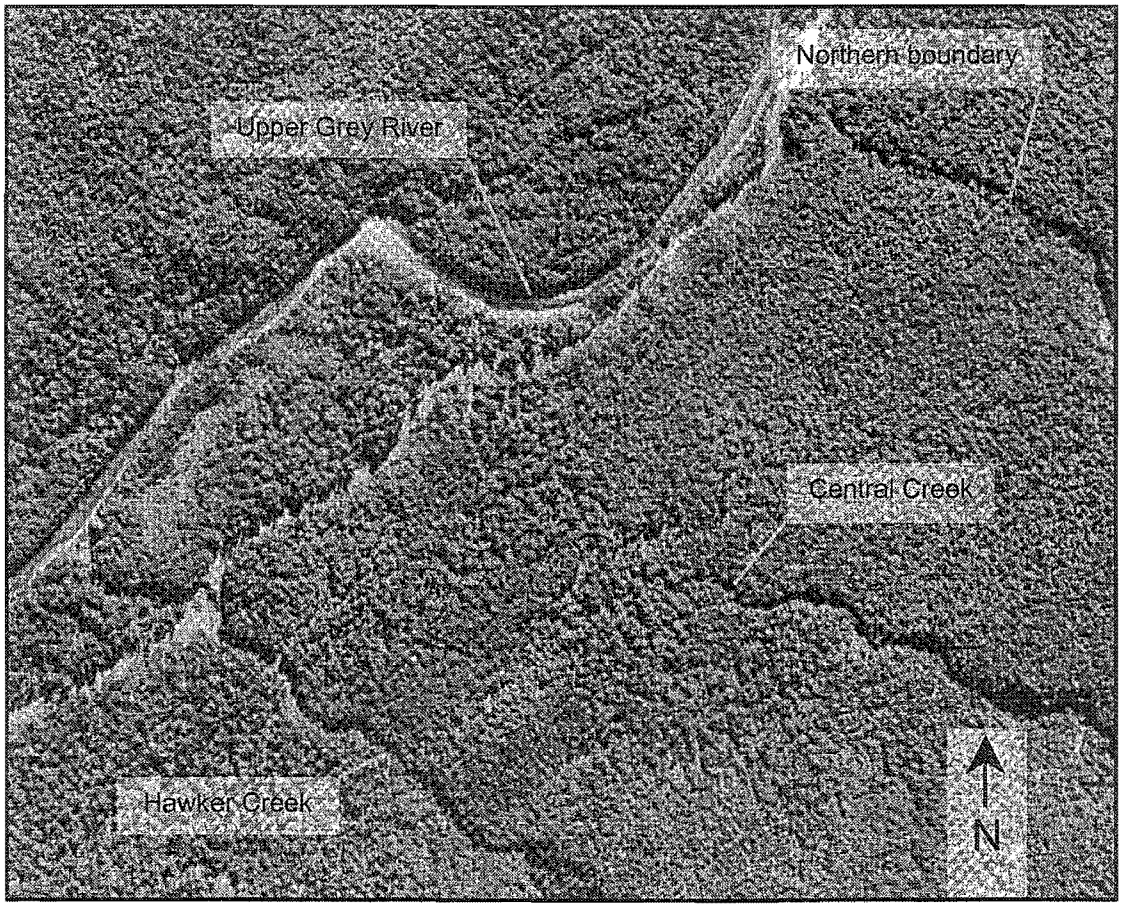

Figure 2.2: Aerial photo of the study site (taken 1996).

2.3 Geology / lithology

The Alpine Fault runs the length of the Upper Grey Valley, separating westward mountains of granite banded gneiss, and eastward mountains of schist and greywacke (Bowen, 1964). The study site straddled the Alpine Fault and was located on postglacial outwash and alluvial gravels, laid down following the decline of the Otiran glaciation 14, 000 years ago (Stevens, 1980). It is likely that the gravels that comprised the terrace were a mixture of local rock types, but the streams that flowed through the site predominately carried schist (Bowen, 1964), which probably lead to schist being the most common terrace constituent.

Factors such as climate, time and topography are more influential towards soil formation than parent material within this region (Mew, 1975). In a general sense, the soils within the study site were comprised of Blackball lowland yellow-brown earths on terraces and Haast high-country podzolised yellow-brown earths on the hill (DSIR, 1969). However, studies of relationships between soil and landform at nearby Mt Harata (Stewart *et al.*, 1993) and in the Inangahua Valley (Mew, 1975) have identified a finer-scale pattern: yellow-brown earths occur on low glacial outwash and post-glacial terraces; steepland soils associated with yellow-brown earths occur on steep terrain; recent soils occur on river flats, gley soils occur on poorly drained surfaces or low terraces; gley podzols occur on flat surfaces of intermediate or high terraces; organic soils can form in small hollows; and podzols can occur on terrace edges.

Given this pattern, the study site predominately comprised yellow-brown earths of varying age on the terrace, podzols on the terrace edges and gley soils in the swamp. The most recent soils occurred immediately adjacent to the Upper Grey River and feeder streams. The next most recent soils occurred on steep terrace risers and debris slopes feeding off the lower hillside. The oldest soils occurred in the flat northern section of the terrace above the escarpment.

2.4 Climate

The broad pattern of rainfall on the West Coast is driven by the prevailing westerly winds. Warm, moisture-laden air from across the Tasman Sea gets orographically

uplifted over the Southern Alps, which results in considerable rainfall to the west of the Alps and decreasing rainfall to the east (Hessell, 1982). Further finer-scale rainfall patterns are primarily influenced by localised topography. The study site receives, on average, 2800 mm of rainfall annually, of which approximately 32 % falls in spring (NZMS, 1984; NZMS, 1985a). At nearby Springs Junction mean annual temperature is 9.5°C, mean maximum January temperature is 21°C and mean minimum July temperature is -1.1°C (NZMS, 1985b). These temperatures were likely to apply to the study site because both sites share the same altitude and are separated by only 15 km.

2.5 General vegetation

Vegetation in the area formed a sequence as follows: high-altitude alpine grasslands were dominated by *Chionochloa* species; steep mid-altitude slopes were dominated by *Nothofagus* species; and lower-altitude river terraces and swamps were also dominated by *Nothofagus* species, but also contained numerous seral and occasional podocarp species (Wardle, 1984). Extensive farmland was located in the valley to the north and south of the study area. The farmland in the north was separated from the study site by several kilometres of *Nothofagus* forest, but that in the south was less than one kilometre away from the study site. The actual study forest was dominated by *N. fusca* and *N. menziesii*, except for swamp areas and the unsealed Palmer Road (Figure 2.2). The roadsides contained abundant *F. excorticata, A. serrata* and introduced grasses, and the swamp was dominated by *Carex secta*. Wind disturbance appeared to be a reasonably common occurrence in the study site, as frequent canopy gaps were present, especially around the toe of the hill. Debris flows and slips were also commonplace. Apart from the obvious discontinuities, forest structure was generally consistent throughout as mature *Nothofagus* trees dominated all but the steepest areas.

2.6 Possum history

Possums were liberated at Springs Junction in 1939 (Pracy, 1974), and it is probable that this is the source of the study site's possum population. Although the number of liberated possums is unknown, it was likely to be between five and ten, as this was

typical for other liberations in the Nelson and Westland regions (Pracy, 1974). Assuming a small number of possums in the initial liberation, there would have been a lag of several years before the population built a dispersal capability. It has been postulated that the rate of colonisation by possums is approximately four kilometres per annum in any direction, as this is the average dispersal distance for juvenile possums in some indigenous forests (Clout and Efford, 1984; Ward, 1985). However, this colonisation rate is potentially an overestimate, as dispersing juvenile possums could be expected to settle earlier when they are colonising unoccupied habitat due to very low competition for resources (Cowan, 2000b). In support of this, Pekelharing and Reynolds (1983) observed colonisation rates of 0.8 km/annum and 1.6 km/annum in Westland National Park and commented that the slower rate could be attributed to denser vegetation and more dissected terrain. Given these colonisation rates, and assuming that no further unrecorded liberations were made along Palmer Road, possums could have reached the study site as early as the early 1950s and as late as the mid 1960s. These estimates of colonisation dates indicate that the resident possum population is currently likely to be at post-peak density, as it generally takes between 25-35 years after colonisation for peak density to occur (Pekelharing and Reynolds, 1983; Thomas *et al.*, 1993).

Prior to the study, approximately 100 possums were removed from the study site between January 1998 and May 1999 for the purpose of an earlier diet study (Cochrane *et al.*, 2003). This was the most significant extraction of possums from within the study site to the author's knowledge. Additionally, control has been carried out by commercial possum hunters operating in the area (D. Lockington, pers. comm.) and possums have been frequently shot along the roadside by locals for either recreation or to fulfil commitments to the Animal Health Board (AHB). The Buller District Council has conducted aerial 1080 drops along roadsides and farm edges as requested and funded by the AHB. Nevertheless, the most recent 1080 drop did not interfere with the course of this study, as possum control within the study site was suspended until the completion of field work for this study. Subsequent possum control within the study site was undertaken by contractors using a combination of leg-hold traps and cyanide, and resulted in a five percent residual trap catch (RTC). This control operation was used to estimate possum density within the study site and provided an estimate of 1.5 possums/ha (Appendix 1).

Several species of introduced mammal, other than possums, were seen within the study area. These included red deer (*Cervus elaphus*), hare (*Lepus europaeus*), cat (*Felis catus*), stoat (*Mustela erminea*), rat (*Rattus rattus*), mouse (*Mus musculus*) and hedgehog (*Erinaceus europaeus*).

Chapter 3: Possum Movements

3.1 Introduction

Animal movement patterns are the product of many discrete and complex choices made at various spatial and temporal scales (Kamil *et al.*, 1987; Crist *et al.*, 1992; Gautestad and Mysterud, 1993). These choices pertain to the need to acquire resources such as food, water, shelter and mates (Drickamer *et al.*, 1996), and also relate to social interaction, predator avoidance and stochastic influences (Drickamer *et al.*, 1996). The relative importance of individual choices is subject to change in response to endogenous and exogenous stimuli, and hence, movement patterns are similarly affected. Ultimately, it is the temporal and spatial distribution of resources or other contributing factors that determines animal movement patterns (Laca and Demment, 1991; Sutherland, 1996).

The most fundamental concept of animal movement pattern is that of home range. Traditionally, home range is defined as the area in which an animal finds most of its resource requirements and spends most of its time (*see review* Kernohan *et al.*, 2001). This definition is highly dependent on time, as home ranges are subject to temporal change in response to changing animal motivations, such as breeding (Ford, 1983). Consequently, home ranges can only be compared with confidence if they relate to the same temporal period (Morris, 1988). The value of a home range is likely related to the animal's knowledge of the distribution of resources within it, as familiarity allows animals to be efficient with their activities (Pough *et al.*, 1996).

Depending on the animal in question, home ranges can sometimes be divided into the sub-units of undefended range, territory and core areas; an undefended range is the area of the home range in which the presence of other individuals is tolerated (Drickamer *et al.*, 1996), a territory is an actively defended area (Morrison *et al.*, 1992) and a core area is one of intense use (Kernohan *et al.*, 2001). The extent of home range overlap between individuals is largely determined by the extent of the undefended area (Drickamer *et al.*, 1996; Pough *et al.*, 1996). Definitions of home range and associated core areas provide valuable information on the behavioural

ecology of a species within different habitats or at different densities (Bekoff and Mech, 1984; Morris, 1988; Drickamer *et al.*, 1996).

The estimation of home range requires temporally staggered acquisition of animal location information over a study period and is most commonly achieved with radio telemetry techniques (Harris *et al.*, 1990; Kernohan *et al.*, 2001). However, the frequency of this location point acquisition is an important consideration, as it influences the reliability of the home range estimate. Factors that influence this frequency include finance, labour constraints and statistical constraints, such as autocorrelation. Finance and labour constraints are restrictive, yet autocorrelation concerns can be managed with knowledge of the biology of the study animal.

Many viewpoints on autocorrelation can be found in the literature (Swihart and Slade, 1985; Harris *et al.*, 1990; Thomas and Taylor, 1990; Alldredge and Ratti, 1992; Aebischer *et al.*, 1993; Rooney *et al.*, 1998; Otis and White, 1999). Autocorrelation occurs when the time periods between consecutive observations of animals are not sufficiently large to render those observations independent of each other and may result in underestimates of true home range size (Swihart and Slade, 1985) or the spurious identification of core areas (Gautestad and Mysterud, 1993). This dependence problem also flows through to statistical analyses performed on animal movements, and can result in significant bias in resource selection studies (Thomas and Taylor, 1990). Nevertheless, Otis and White (1999) argue that the autocorrelation problem can be avoided if location sampling is achieved in a stratified standardised approach within an ecologically significant time period, such as one that reflects cycles of behaviour. Locations sampled in this manner represent an unbiased sample of an animal's movement trajectory through the landscape over the study period (Aebischer *et al.*, 1993; Otis and White, 1999).

Knowledge of possum ranging behaviour has many implications for pest management. Once described, movement patterns can be incorporated into strategies designed to provide adequate spacing of poison, traps or other monitoring equipment (Kolb, 1984; Thomas *et al.*, 1984; Green and Coleman, 1986; Moller *et al.*, 1996; Edwards *et al.*, 2000; Miller *et al.*, 2001). Home range components such as maximum range lengths and overall range size are important considerations, as they influence

the likelihood of encounter between an animal and control or monitoring units at a given spacing regime (Cowan and Clout, 2000; Edwards *et al.*, 2001). As such, investigation of these movement parameters has the potential to improve efficiencies of control and monitoring operations.

The movement patterns of possums are highly plastic (Kerle, 1984) and are influenced by both the biotic and the abiotic environment (Green, 1984). Non-dispersing possums have been observed to travel regularly up to 1.2 km through forest to graze in pasture (Green and Coleman, 1986) and up to 1 km through continuous *Nothofagus* forest (Clout and Gaze, 1984). They have also been observed travelling similar distances to feed on seasonally available foods in other areas (Jolly, 1976; Ward, 1978). Conversely, some studies have demonstrated that possums are sessile, occupy small home ranges and infrequently range more than a few hundred metres (Crawley, 1973; Thomas *et al.*, 1984; Cowan and Rhodes, 1993; Brockie *et al.*, 1997).

This substantial variability observed in possum movements limits the validity of extrapolating possum movement parameters from one site to another. For example, if the large range lengths observed for possums in pastoral complexes (e.g. Green and Coleman, 1986) were used as the basis for trap spacing in a lowland broad-leaved/podocarp forest, a considerable proportion of the population would have a low probability of trap encounter due to their smaller range lengths (e.g Ward, 1978). Control or monitoring devices need to be spaced with respect to the smallest home range size if all animals are to have a reasonable probability of encounter (Moller *et al.*, 1996). For this reason, explicit knowledge of possum movement patterns in all vegetation types is necessary if control and monitoring strategies are to be optimised.

Differences between possum home ranges in different areas are likely attributable to resource quality and dispersion, and population size in relation to carrying capacity (McNab, 1963; Harestad and Bunnell, 1979; Schoener, 1981; Ford, 1983). This relationship is complex because population size and resource quality are not independent. Hypotheses such as the resource dispersion hypothesis (RDH) and the food-exploitation hypothesis (FEH) have been postulated to account for the relationship between resource quality and dispersion, and home range size in

carnivores and herbivores, respectively (Macdonald, 1983; Larter and Gates, 1994). Specifically, both of these hypotheses predict that animals occupying poorer quality habitats will have larger home ranges. Indeed, this pattern has been demonstrated for numerous species of carnivore, herbivore and omnivore (Geffen *et al.*, 1992; Hulbert *et al.*, 1996; Tufto *et al.*, 1996; Gehrt and Fritzell, 1997). As such, it is likely that possum home range size within the Palmer Road study site will be dependent on localised resource (vegetation) quality. Furthermore, it is possible that possum home range sizes will change in response to the changing availability of seasonally exploitable food resources, as these food types will modify both resource quality and resource dispersion.

The objectives of this chapter are to:

- Describe the movements of radio-tracked possums within the study site in terms of home range size and shape, and range length at multiple temporal scales.
- Compare these parameters to those obtained in other studies.

The movement parameters observed in this study will then be used in subsequent chapters to relate possum movements with resource distribution at multiple spatiotemporal scales.

3.2 Methods

3.2.1 Radio-tracking

Between December 1999 and January 2000 12 possums were captured within the study site. Of the 12 possums sampled, the first two were caught with cage traps baited with apple and the remaining 10 were caught using Victor® no.1 leg hold traps using flour, icing sugar and raspberry essence as lure. Most trapping effort was focused on the roadside and streamside areas, as possum sign was sparse throughout the main terraces. An approach using a regular trapping grid and random selection of trapped possums would have been preferable, but would have been logistically infeasible given financial, labour and time constraints.

Possums were subdued in a sack after capture and were then fitted with mortality-sensing 2-stage possum radio transmitter collars that operated within the 160 – 161 MHz frequency range (Sirtrack, 1999). These collars weighed 33 g, which represented 1.3 % of average possum body weight. Radio-tracking was conducted using Telonics TR-4 receivers and Sirtrack's hand-held 3-element Yagi antennae (Sirtrack, 1999).

Radio-tracking occurred six times at bi-monthly intervals starting from early March 2000 and ending early January 2001. On each of these six occasions, possums were radio-tracked for three fine days. Wet days were not utilised because possums have been observed to modify their behaviour in wet weather (Ward, 1978) and such a modification would have introduced bias between tracking outings. Den sites were recorded for each tracking day, as were the locations of active possums at three times during the night at three-hourly intervals during the longer nights of winter and at two-hourly intervals during the shorter nights of summer. These time intervals were chosen in order to sample activity evenly throughout the night. Radio-tracking commenced two or three hours after dark because possums tend to be relatively inactive for the first few hours after emerging from the den (Ward, 1978; MacLennan, 1984).

3.2.2 Autocorrelation

In view of Otis and White's (1999) guidelines, autocorrelation is not considered a concern for this study for three reasons:

1. The annual period of this study has ecological significance, as possum movement patterns are annually stable (Crawley, 1973; Jolly, 1976; Ward, 1978; Brockie *et al.*, 1989);
2. Within this time period radio-tracking has been divided into evenly spaced strata of seasons, days and hours;
3. Individuals are used as experimental units.

3.2.3 Location acquisition and recording

Providing accurate locations of study animals is difficult but necessary and can be achieved using several different approaches. A trial of triangulation as a means for location sampling was undertaken to test its applicability to the study area. This method requires the synchronous collection of angular bearings to a signal source from two or more different positions; the intersection of these bearings gives the estimated location of the animal (Saltz and Alkon, 1985). Errors for the estimate can then be computed by incorporating the error arcs of angular bearings, which are principally composed of bias or system error and sampling error (Saltz and Alkon, 1985). At the study site, the system errors were found to be very large, and were primarily attributable to signal deflection from trees. Subsequently, many of the calculated error polygons were unacceptably large, and in some cases were open-ended. In light of these results, it was decided that radio-tracking to within close range of individual possums was a more desirable approach, as it significantly decreased the likelihood of location estimate errors.

Close range radio-tracking presented its own problems. Initial trials of close radio-tracking resulted in the disturbance of possums and introduced a likely bias in their behaviour. To remedy this, it was decided to track to within no less than 30-40 m, which was considered distant enough to avoid disturbance. This was achieved by noting the signal strength at various distances from the source during the initial trial and using this to gauge proximity to the animal being tracked. Once a possum was tracked to within close range, the actual location of the possum was difficult to estimate because of the lack of easily visible landmarks within the terrace forest at night. Because of the limitations of using global positioning system (GPS) under a forest canopy (Rempel *et al.*, 1995; Moen *et al.*, 1996), a recording system was developed for this study based on 0.5 ha grid cells. This grid was superimposed on a magnified topographic map of the study area and landmarks were created by referencing existing landmarks such as standing trees, windfalls and bends in streams, and by creating new landmarks by putting out flagging tape in key areas during the day. This network of landmarks was sufficient to provide accurate locations of radio-tracked possums within the forest at night.

Location estimates always carry with them an error component, although its magnitude is seldom reported and even more infrequently included in analyses (Nams, 1988; Harris *et al.*, 1990; Saltz, 1994). Recording locations as grid cell references has the advantage of incorporating this error component within each location estimate. This error component was likely to be less than the 0.5 ha cell area because, as previously stated, possums were tracked to within close range and the use of landmarks enhanced location accuracy. Another intuitive advantage of the grid cell method is the recognition that animals tend to select mosaics, not discrete points (Rettie and McLoughlin, 1999).

3.2.4 Home range analysis

Home range analysis was performed on animal locations using the Animal Movement extension in Arcview GIS 3.2a (ESRI, 2001). The kernel method of home range estimation was chosen because it has several desirable properties; it uses non-parametric techniques that allow it to describe a wide range of distribution patterns, it identifies core areas well, and when used in a GIS environment allows probability contours to be plotted (Worton, 1989; Seaman *et al.*, 1998). This method makes use of more information than the minimum convex polygon (MCP) method by calculating a utilisation distribution, as opposed to just circumscribing an area around some of the most extreme points (Southwood, 1966). Although the MCP method is useful for comparisons across studies, it is strongly influenced by peripheral fixes and may include areas that an animal never uses (Harris *et al.*, 1990; Kernohan *et al.*, 2001). For these reasons, the MCP method was only used to allow comparison with annual home ranges estimated in other studies.

Home range calculations are preformed on point location data (Worton, 1989; Harris *et al.*, 1990) and, as such, location references from the grid recording system required conversion to discrete points before home range calculation could proceed. Initially, location references were entered as midpoints of the 0.5 ha cells within an Arcview GIS 3.2a database. These points were then randomly redistributed within cells in which they occurred for 100 replicate data sets in order to incorporate location error into home range calculations. Calculation of kernel home ranges requires a smoothing parameter to be selected (Worton, 1989), the choice of which critically

influences the size of the home range (Harris *et al.*, 1990). This choice was made objective by using the least squares cross validation technique (LSCV), which seeks to minimise estimated error for a given sample (Seaman *et al.*, 1998).

Home range size was defined as the area encompassed by the 95 % probability contour as determined by the kernel method. The length of that range was defined as the longest length across the 95 % contour. Annual, bi-monthly, and three-day home range sizes and lengths were estimated for each possum.

Investigation into the influence of the number of observations on home range size was undertaken to establish suitable sample sizes for analysis. Average home range size was calculated for increasing numbers of consecutive radio-tracking fixes and these data were plotted in order identify the number of fixes above which home range calculation became stable.

3.2.5 Statistical analysis

Non-parametric statistical techniques were used because of the low number of possums sampled and because of the inherent variability of possum behaviour. These factors likely render the assumption of normality invalid, and hence, compromise the validity of parametric techniques (Daniel, 1990).

Temporal differences in home range size were tested with the Wilcoxon matched-pairs signed-ranks test. This powerful test compares different home ranges of the same possum (Daniel, 1990), thereby avoiding bias problems associated with pooled data. The relationship between weight and sex, and the relationship between home range size and sex was tested using the Mann-Whitney test (Daniel, 1990). The Spearman rank correlation coefficient was use to test the relationship between body weight and home range size (Daniel, 1990).

3.3 Results

For descriptive purposes individual possums are referred to by their radio-collar channel number. The capture locations of the twelve radio-collared possums are shown in Figure 3.1.

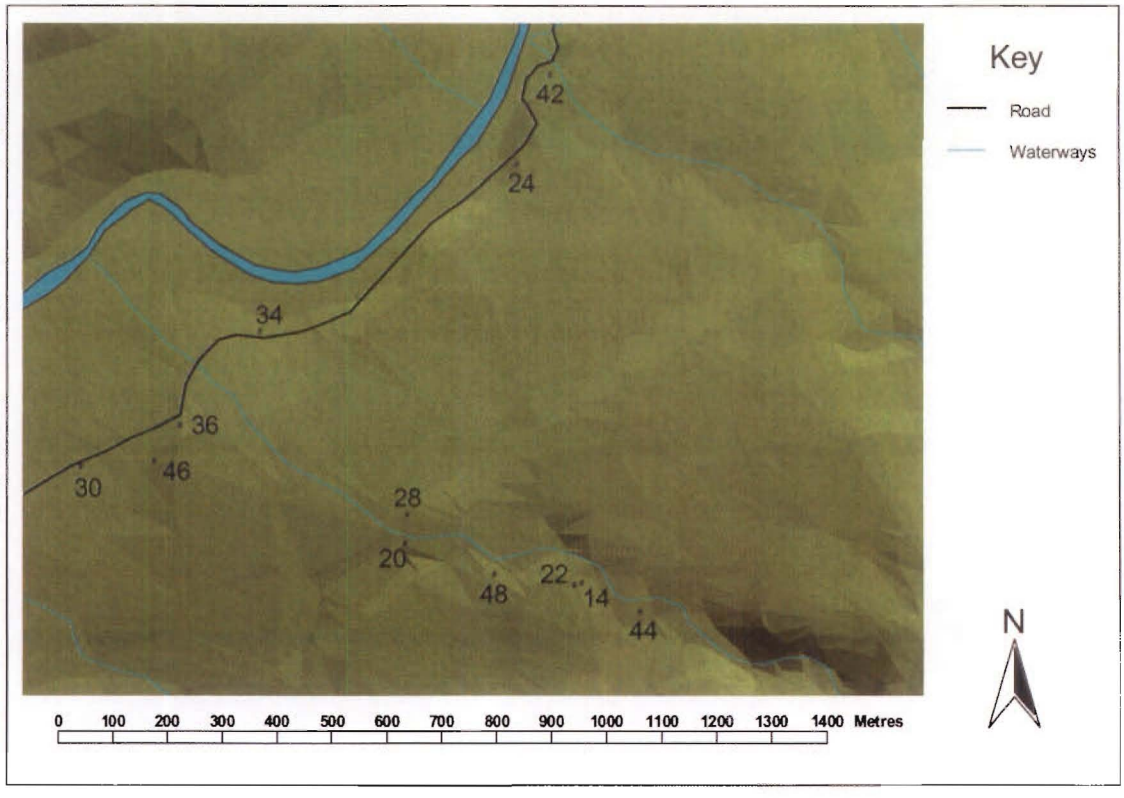

Figure 3.1: Capture locations of sample possums. Channel numbers are used to identify individuals.

3.3.1 Sample possums

Despite the lack of complete randomness, the sample represented the population well; there was an even split of males to females, juveniles and senescent adults were represented, and the sample covered the full range of habitats in the study area. No significant difference was detected between the sexes regarding weight using the Mann-Whitney test ($P > 0.15$). However, the average weight of males was 2.5 ± 0.3 kg (mean ± s.e.), the average weight of females was 2.7 ± 0.1 kg and the average combined weight was 2.6 ± 0.2 kg, range 1.3 - 3.2 kg (Table 3.1).

Table 3.1: Channel number, sex and weight of sample possums.

Channel number	Sex	Weight (kg)
14	Male (juvenile)	1.3
20	Female	2.7
22	Female	3.0
24	Female	2.9
28	Male	2.5
30	Male	3.0
34	Female	2.4
36	Female	2.7
42	Male	2.1
44	Male	2.8
46	Male	3.2
48	Female	2.5

3.3.2 Loss of sample possums

Four of the twelve possums died during the course of the study. Possum 20 died between the July and September telemetry outings. This possum was an old female and appeared to be infested with fur mites as it had lost a great deal of fur from its back and tail. It was found beside a fallen log alongside Central Creek and appeared to have died of natural causes. At the commencement of the November telemetry, possum 30 could not be located and was presumed dead, also possum 42 was found dead on the road and appeared to have been shot. Possum 28 was the final possum to be killed and was found shot at the roadside at the commencement of the January telemetry.

Dispersal behaviour was exhibited by one of the sampled possums. The juvenile possum 14 spent the first seven months of the study near its mother, possum 22, but at the commencement of the July radio telemetry, possum 14 was found to have moved around the face of the hillside towards Hawker Creek. Over the next two nights this direction of movement was maintained as it travelled out of the study site and into the upper reaches of Hawker Creek. A relocation attempt in September 2000 indicated that this possum had dispersed approximately 2 km from its natal site.

No evidence was found to suggest that predation other than spotlighting along the roadside had occurred.

3.3.3 Home range

Average home range size appeared to stabilise after approximately 25 consecutive fixes (Figure 3.2). This indicates that the number of fixes obtained during each three-day radio telemetry excursion (mean 13) was insufficient to define possum home ranges completely. To avoid potential bias that this effect may introduce, the minimum number of fixes used to define home range with kernel estimation should be approximately 30 (Seaman *et al.*, 1999). For this reason, three groups of two months were amalgamated for analysis; they were March/May, July/September and November/January. Although this accounts for only 26 fixes per individual per season, further amalgamation would render comparisons inconsequential.

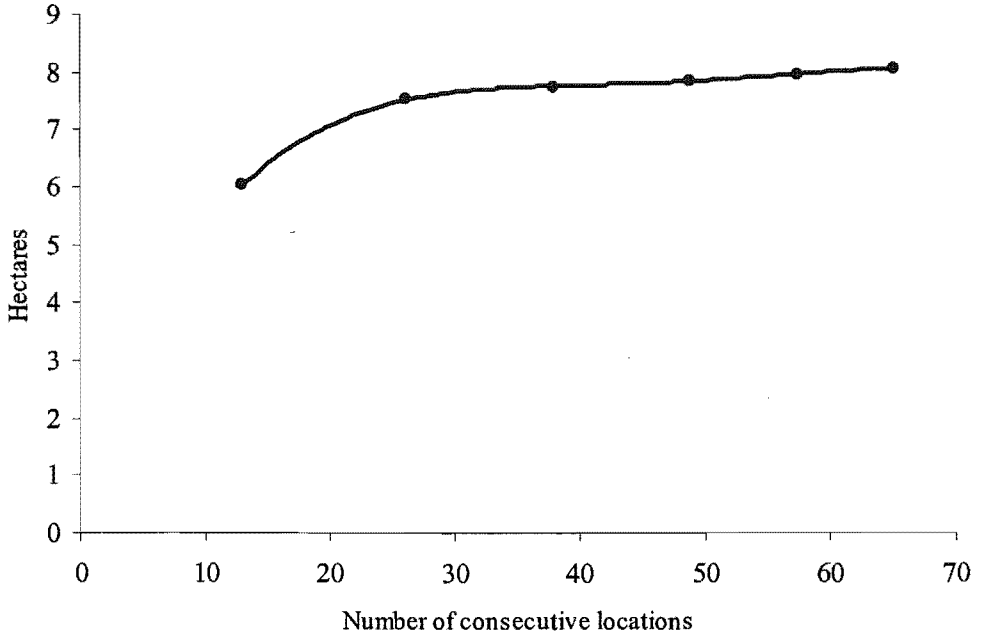

Figure 3.2: Cumulative effect of sample size on average home range size calculated with the kernel method.

No significant difference was detected in annual home range size, calculated with the kernel method, between the sexes ($P>0.1$) and no significant relationship was detected

between annual home range size, calculated with the kernel method, and body weight ($P>0.1$), as predicted by the resource dispersion hypothesis (RDH). The average annual home range area for all possums, calculated with the kernel method, was 8.07 ± 0.99 ha (range 4.22 – 15.36 ha). These figures closely match those obtained using the MCP method of home range classification (7.63 ± 1.55 ha, range 3.10 – 21.51 ha). The kernel method produced smaller annual home ranges for possums that ranged widely (e.g. possum 46), yet produced larger annual home ranges for sedentary possums (e.g. possum 24) when compared to the MCP method. No such relationship was observed for the three-nightly home ranges, as the kernel method provided consistently larger ranges. Three-nightly home ranges were much more consistent across individuals than those calculated annually.

Table 3.2: Home range sizes in hectares (mean ± s. e.). The bi-monthly scale represents the combined months (March and May, July and September, and November and January) and the three-nightly scale represents the fixes obtained for each radio-tracking outing. Home ranges were not calculated for nightly radio-tracking fixes because sample sizes were too small to provide robust home range estimates.

Possum	Annually		Bi-monthly		Three-nightly	
	MCP	Kernel	MCP	Kernel	MCP	Kernel
14*	4.75 ± 0.06	5.80 ± 0.06	4.14 ± 0.05	4.37 ± 0.04	2.04 ± 0.21	3.43 ± 0.37
20†	6.50 ± 0.10	7.37 ± 0.08	4.80 ± 1.78	3.70 ± 0.71	2.06 ± 0.70	3.42 ± 0.68
22	5.29 ± 0.06	6.63 ± 0.06	3.96 ± 0.64	4.50 ± 0.38	1.38 ± 0.30	3.08 ± 0.28
24	3.48 ± 0.05	5.13 ± 0.04	2.49 ± 0.60	3.24 ± 0.39	0.87 ± 0.13	2.39 ± 0.17
28‡	10.37 ± 0.08	11.47 ± 0.10	6.10 ± 1.35	4.45 ± 0.65	3.39 ± 0.72	3.98 ± 0.22
30§	6.44 ± 0.06	7.96 ± 0.23	5.02 ± 1.10	4.63 ± 0.16	1.82 ± 0.63	3.27 ± 0.30
34	3.81 ± 0.07	5.80 ± 0.05	1.80 ± 0.32	2.61 ± 0.17	0.71 ± 0.13	2.23 ± 0.20
36	10.84 ± 0.09	10.84 ± 0.08	7.29 ± 2.40	4.90 ± 0.65	2.16 ± 0.41	3.55 ± 0.33
42§	12.23 ± 0.09	11.41 ± 0.09	8.75 ± 3.61	5.67 ± 0.80	2.49 ± 0.39	3.79 ± 0.17
44	4.44 ± 0.05	4.83 ± 0.06	2.82 ± 0.60	3.61 ± 0.37	1.09 ± 0.17	2.58 ± 0.12
46	21.51 ± 0.14	15.36 ± 0.09	9.31 ± 1.25	5.41 ± 0.63	2.94 ± 0.81	3.44 ± 0.34
48	3.10 ± 0.05	4.22 ± 0.05	2.32 ± 0.22	3.09 ± 0.13	0.96 ± 0.19	2.47 ± 0.24
Mean	**7.73 ± 1.55**	**8.07 ± 0.99**	**4.90 ± 0.72**	**4.18 ± 0.27**	**1.83 ± 0.25**	**3.14 ± 0.17**

*March and May only. † March, May and July only. § March, May, July and September only.
‡ March, May, July, September and November only.

Comparison of the shared area between the three-nightly, bi-monthly and annual home ranges indicates that, on average, over half of annual home range is shared by

bi-monthly home range, approximately 30-40 % of annual home range is shared by three-nightly home range, and 40-80 % of the bi-monthly home range are shared by three-nightly home range (Table 3.3). Possums with lower shared area between the different scales can be said to have lower temporal site fidelity because they exhibit more variable ranging behaviour than those possums with a higher degree of shared area. Possums exhibited considerable variation in nightly and three-nightly range lengths with a range of 24 m (possum 20, March) to 477 m (possum 36, March), and 90 m (possum 34, May) to 638 m (possum 20, May), respectively.

Table 3.3: Shared areas of home ranges at different temporal scales. Shared areas are given as percentages of the first listed scale in the last listed scale. The bi-monthly scale represents the combined months (March and May, July and September, and November and January) and the three-nightly scale represents the fixes obtained for each radio-tracking outing.

Possum	Bi-monthly in annual		Three-nightly in annual		Three-nightly in bi-monthly	
	MCP	Kernel	MCP	Kernel	MCP	Kernel
14	87	75	43 ± 5	59 ± 6	49 ± 13	78 ± 9
20	74 ± 27	50 ± 10	32 ± 11	46 ± 9	43 ± 11	92 ± 18
22	75 ± 12	68 ± 6	26 ± 6	46 ± 4	35 ± 11	68 ± 6
24	71 ± 17	63 ± 8	25 ± 4	47 ± 3	35 ± 8	74 ± 5
28	59 ± 13	39 ± 6	33 ± 7	35 ± 2	46 ± 13	89 ± 5
30	78 ± 17	58 ± 2	28 ± 10	41 ± 4	24 ± 10	71 ± 6
34	47 ± 8	45 ± 3	19 ± 3	38 ± 3	40 ± 9	85 ± 8
36	67 ± 22	45 ± 6	20 ± 4	33 ± 3	30 ± 9	72 ± 7
42	72 ± 30	50 ± 7	20 ± 3	33 ± 2	28 ± 8	67 ± 3
44	64 ± 13	75 ± 8	24 ± 4	53 ± 2	39 ± 8	72 ± 3
46	43 ± 6	35 ± 4	14 ± 4	22 ± 2	32 ± 9	64 ± 6
48	75 ± 7	73 ± 3	31 ± 6	58 ± 6	41 ± 11	80 ± 8
Mean	**67 ± 4**	**56 ± 4**	**26 ± 2**	**43 ± 3**	**37 ± 2**	**76 ± 3**

Nightly movements of over 400 m were exhibited by possums 20, 24, 28, 36 and 46.

Table 3.4: Maximum range lengths for all possums (mean ± s.e.). Range lengths are not given for the combined months because the decision to combine months was related purely to statistical concerns regarding the calculation of home ranges.

Possum	Range lengths (m)		
	Nightly	Three-nightly	Annually
14	235 ± 22	254 ± 15	310 ± 4
20	169 ± 48	349 ± 123	754 ± 4
22	181 ± 13	255 ± 12	371 ± 3
24	156 ± 18	235 ± 39	391 ± 3
28	204 ± 24	346 ± 36	508 ± 3
30	167 ± 20	257 ± 39	390 ± 2
34	115 ± 11	178 ± 24	348 ± 3
36	229 ± 24	324 ± 57	607 ± 3
42	242 ± 22	419 ± 26	515 ± 3
44	160 ± 14	202 ± 23	385 ± 3
46	242 ± 28	372 ± 50	629 ± 3
48	144 ± 15	190 ± 18	267 ± 3
Mean	**189 ± 12**	**282 ± 23**	**456 ± 42**

Mean home range size was found to be significantly larger in the combined March/May season than for the combined July/September season ($P < 0.05$). No other significant bi-monthly group differences were observed.

Home ranges of individuals overlapped extensively (Figure 3.3), especially for possums 14, 22, 44 and 48, which were located in the south east of the study site.

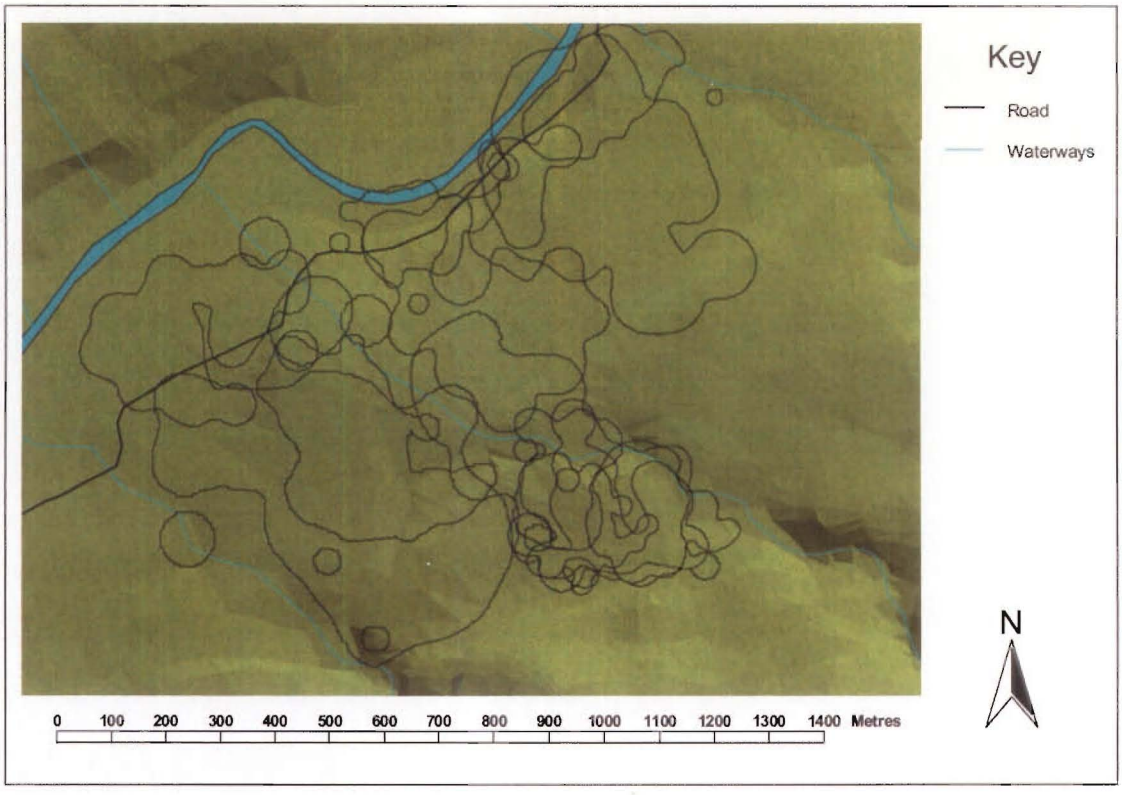

Figure 3.3: An example of 95 % probability contours for all possum home ranges calculated with the kernel method using one random replicate of the cell-midpoint data.

Examples of home ranges based on one randomised replicate of the cell-midpoint data are given in Figure 3.4 to Figure 3.15. Home ranges incorporated all fixes and were calculated using the kernel method with individual LSCV selection of the smoothing parameter. Probability contours are given as 50 and 95 % (i.e. the contours that encapsulate 50 and 95 % of the fixes, respectively). Despite being classified as annual home ranges, the temporal scale of home ranges is finer due to dispersal for possum 14 and mortality for possums 30, 42, 20 and 28.

Possums 14, 22, 44 and 48 were quite sedentary, occupying the upper reaches of the terrace where it met the lower hillside (Figure 3.4, Figure 3.6, Figure 3.13 and Figure 3.15). The home ranges of these possums were fairly uniform and exhibited no strong bias towards movement in any direction. However, the core areas, represented by the 50 % probability contour, of possums 22, 44 and 48 indicate a bias of utilisation towards the incised slopes leading into the central stream, when compared to the more general 95 % probability contours. Possums 24 and 34 were similarly sedentary, but were located along the northern roadside (Figure 3.7 and Figure 3.10). These

possums did show bias in utilisation along the length of the road and core areas were centred on the roadside. Possums 28, 30 and 42 also made use of roadside areas, but in contrast made extensive use of the terrace forest areas (Figure 3.8, Figure 3.9 and Figure 3.12).

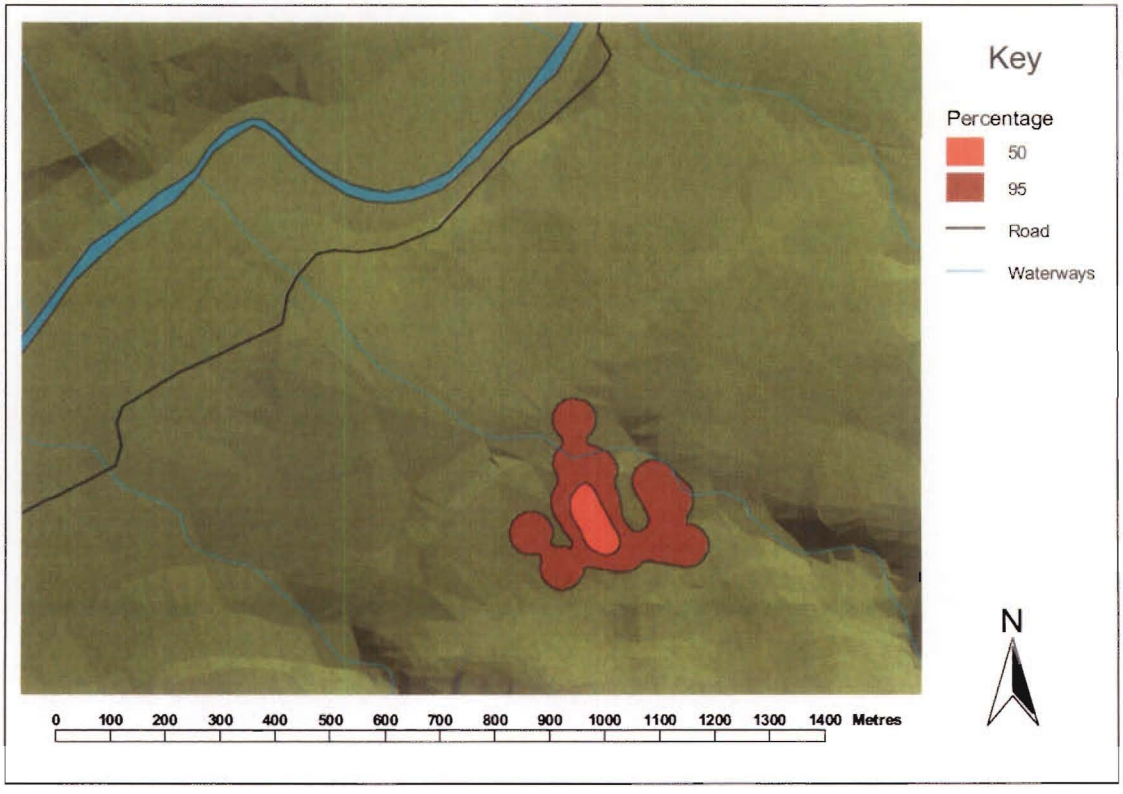

Figure 3.4: Home range of possum 14.

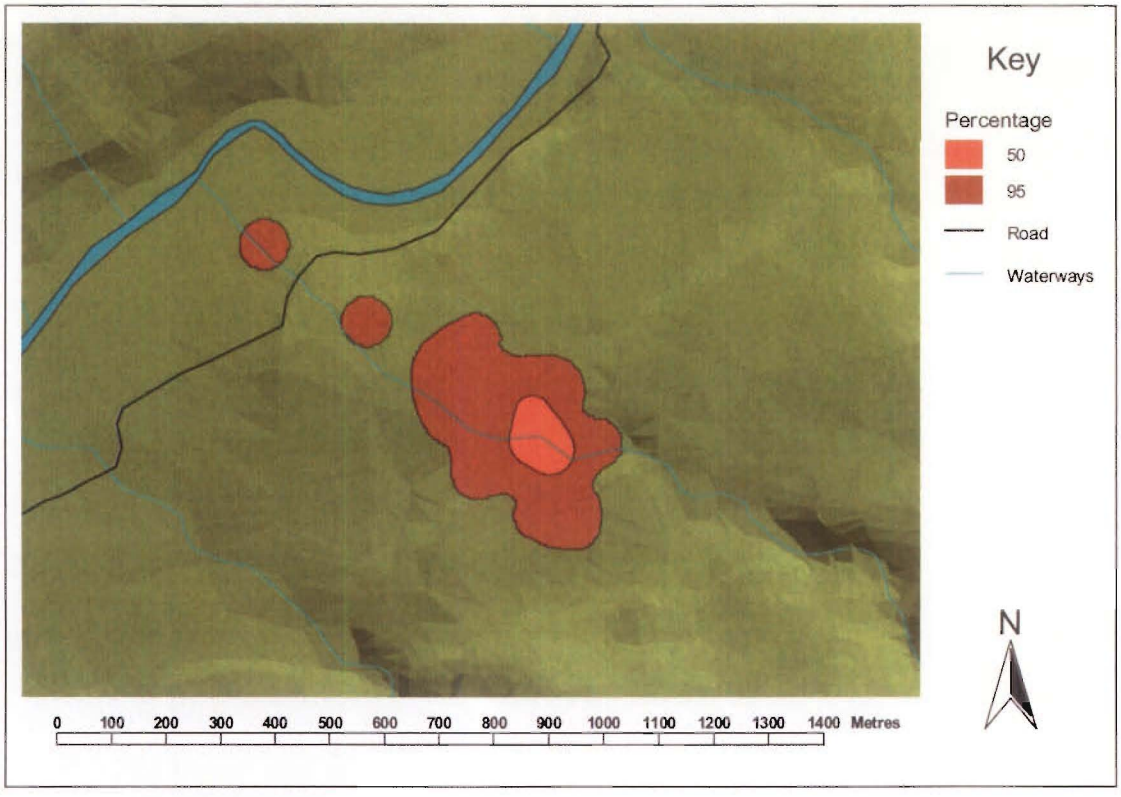

Figure 3.5: Home range of possum 20.

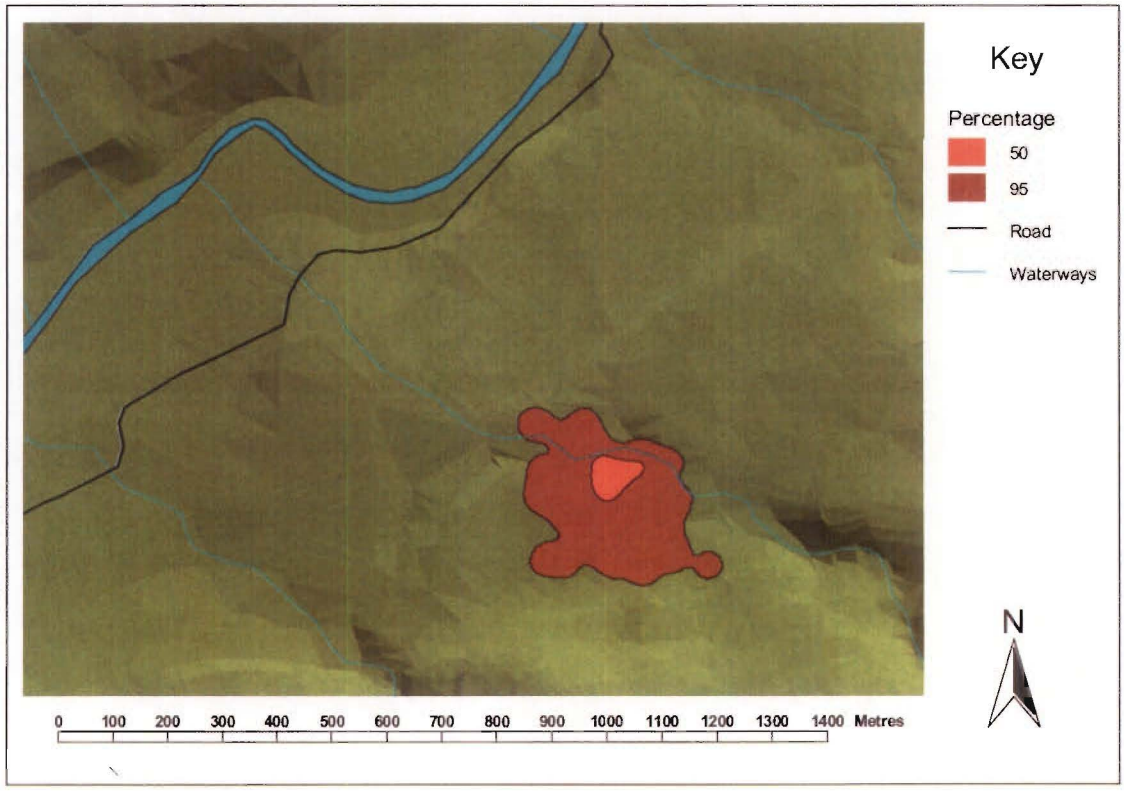

Figure 3.6: Home range of possum 22.

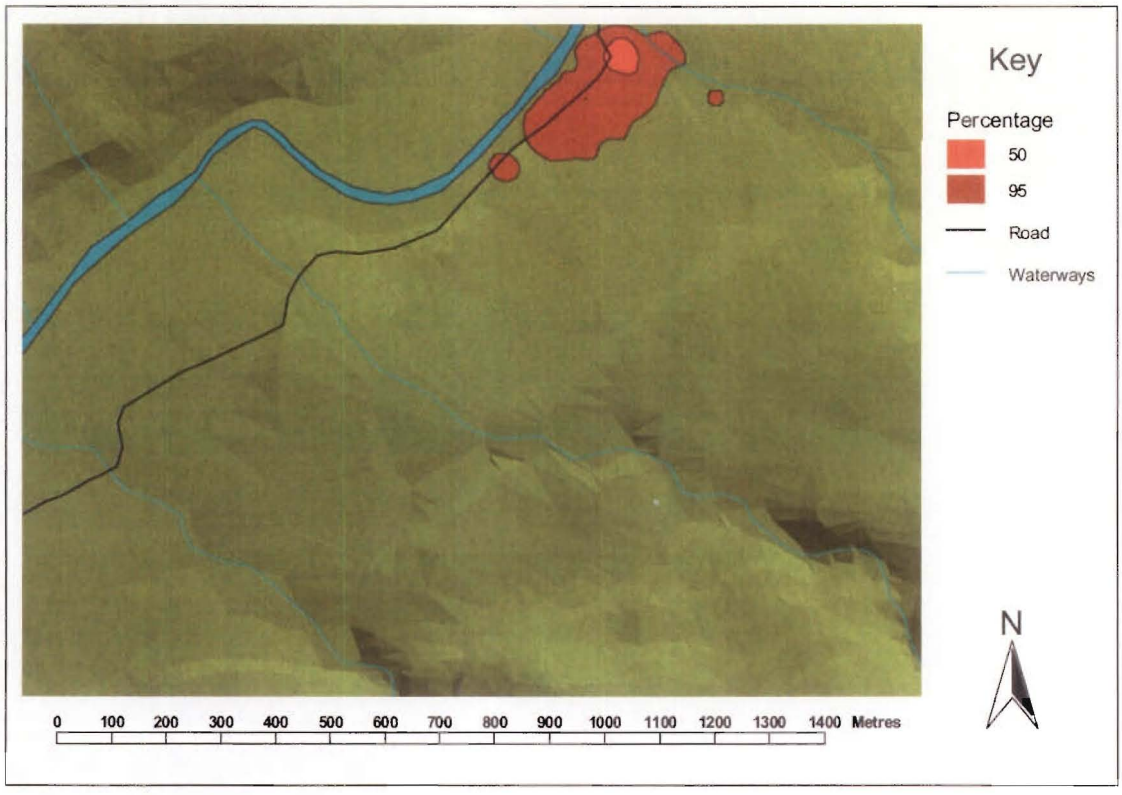

Figure 3.7: Home range of possum 24.

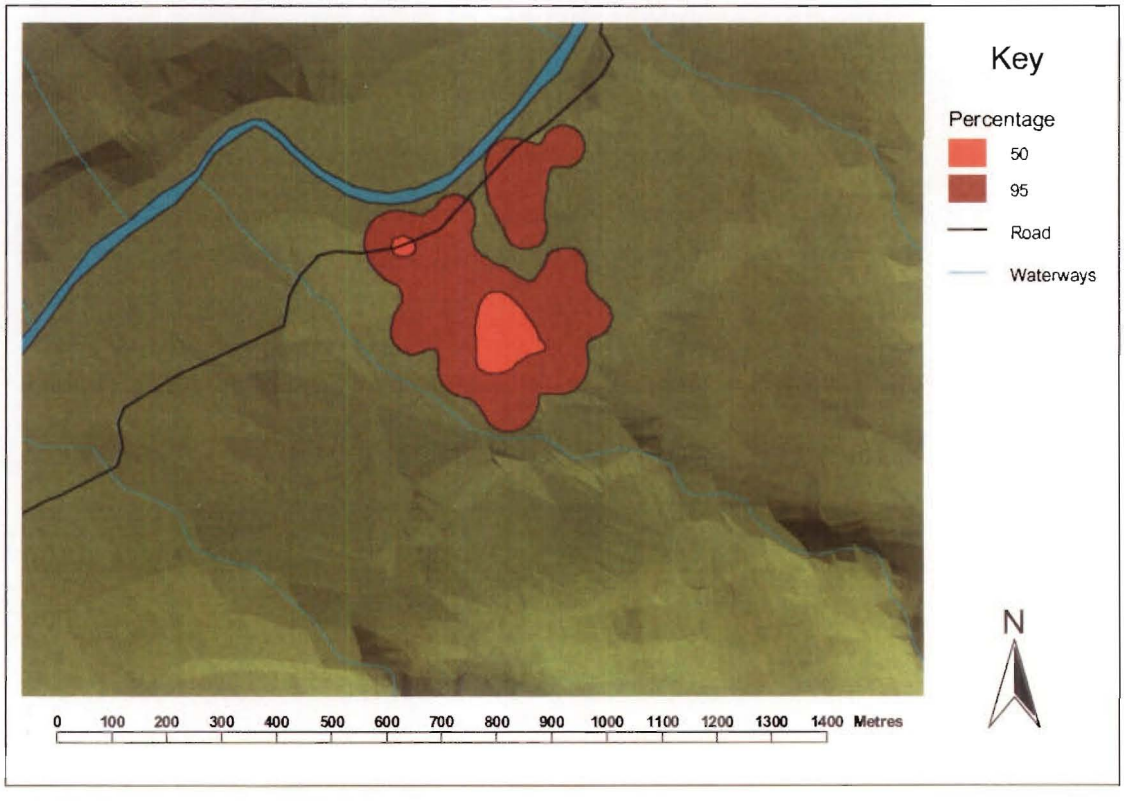

Figure 3.8: Home range of possum 28.

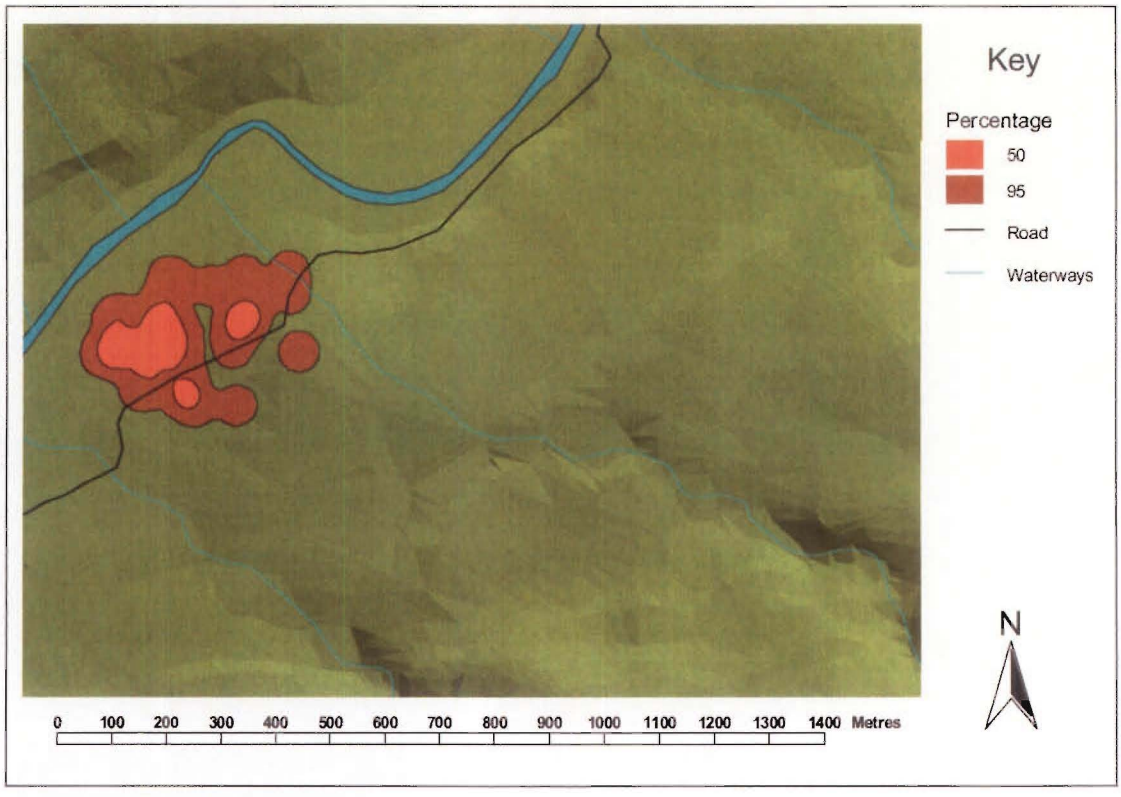

Figure 3.9: Home range of possum 30.

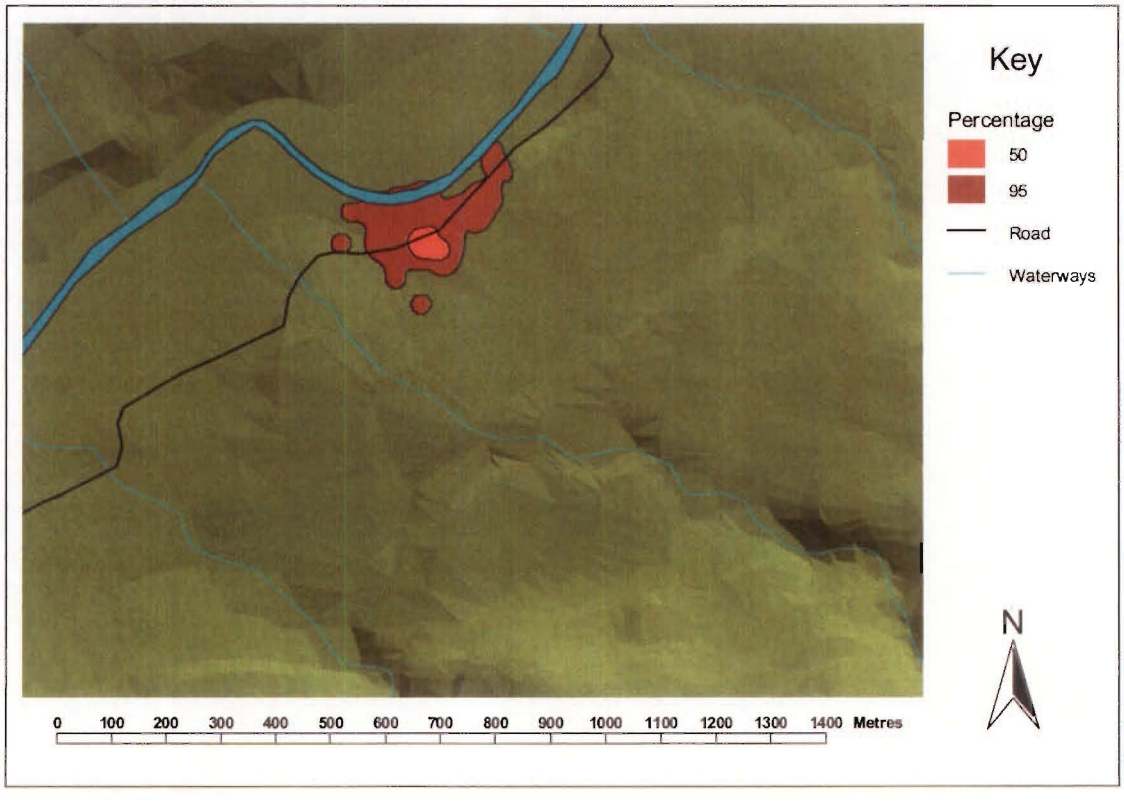

Figure 3.10: Home range of possum 34.

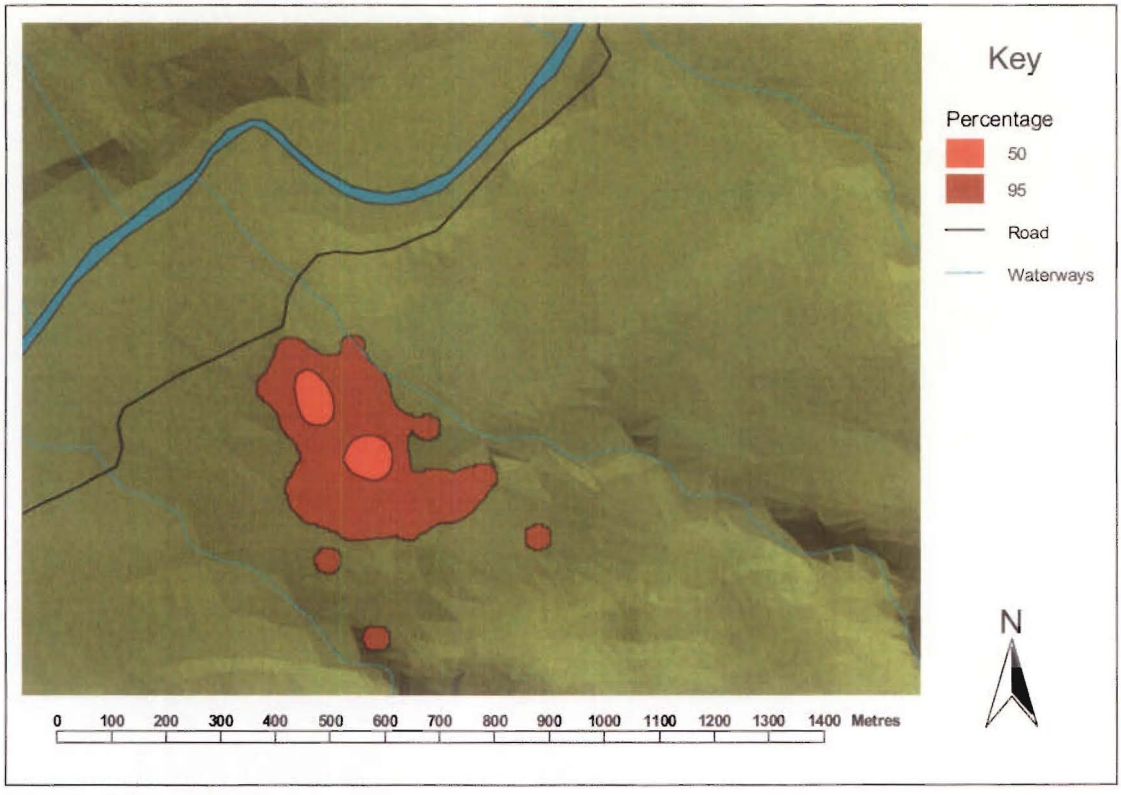

Figure 3.11: **Home range of possum 36.**

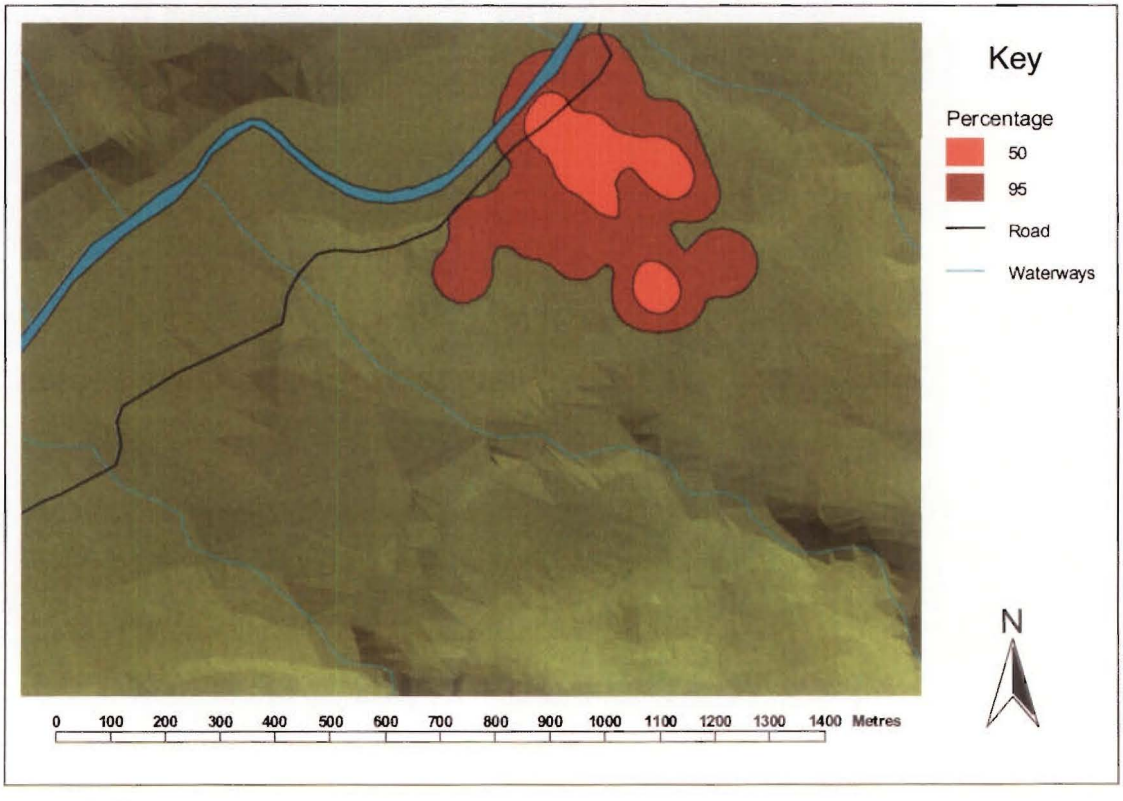

Figure 3.12: **Home range of possum 42.**

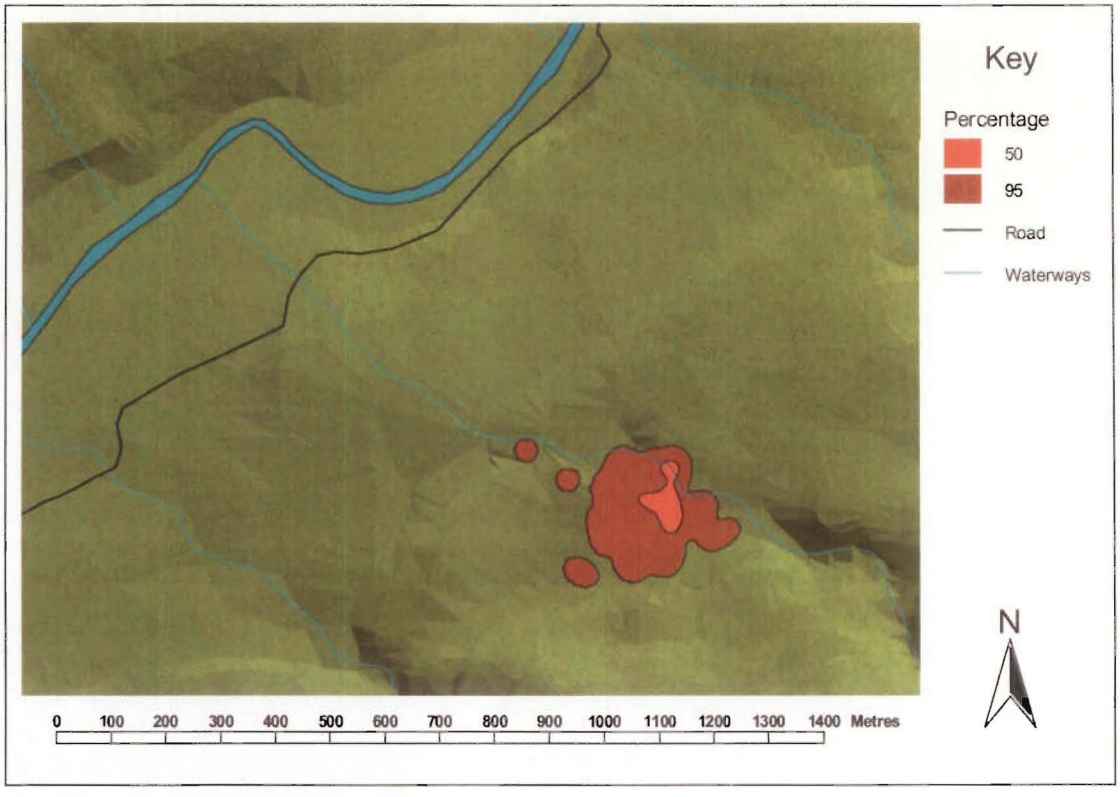

Figure 3.13: **Home range of possum 44.**

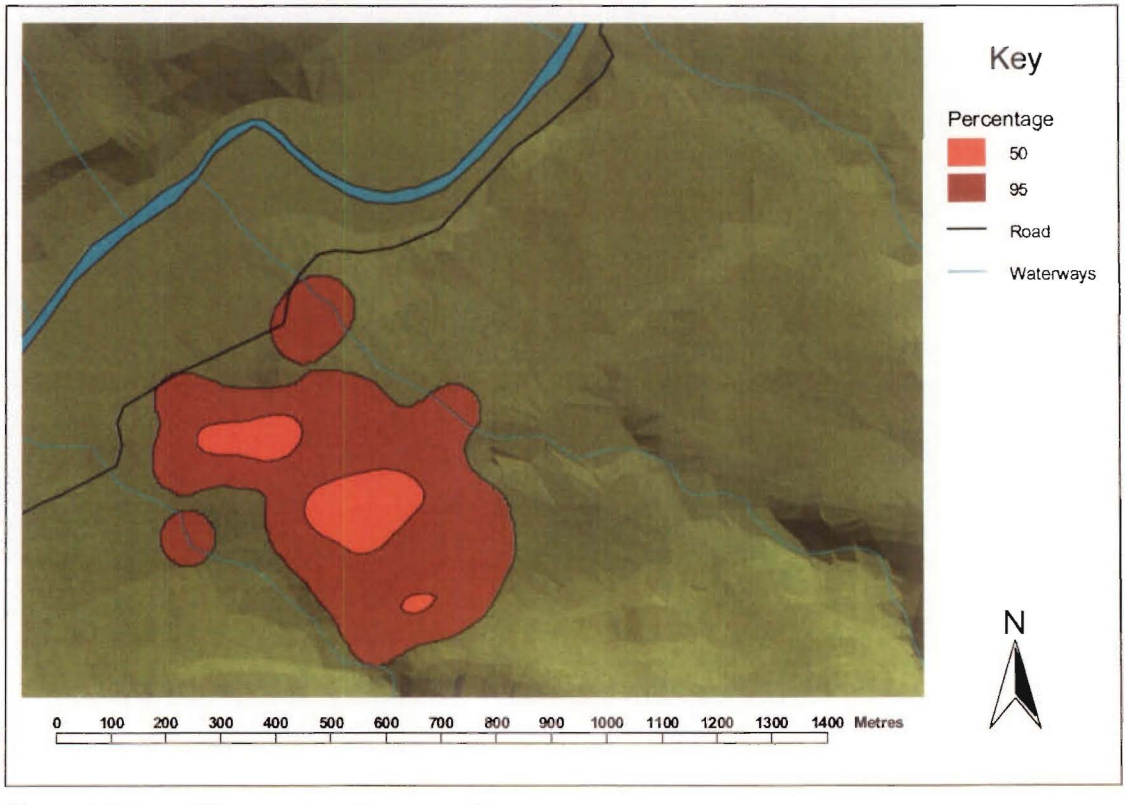

Figure 3.14: **Home range of possum 46.**

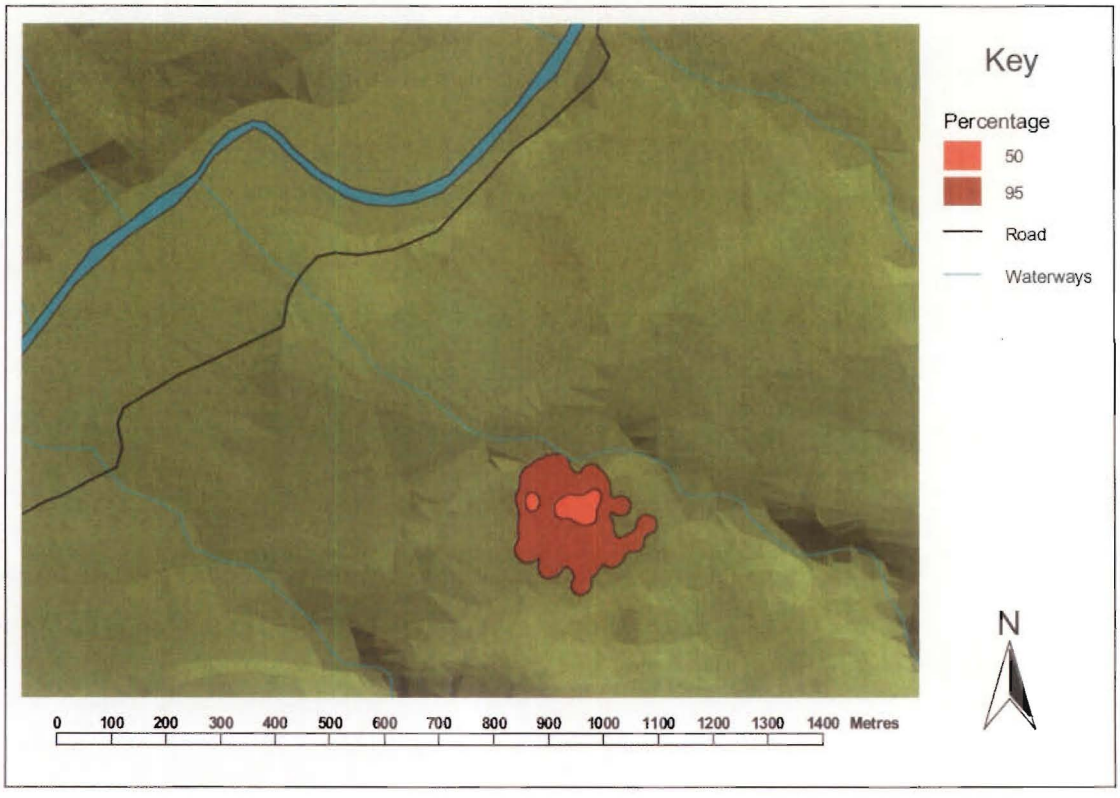

Figure 3.15: Home range of possum 48.

Possums 28 and 42 displayed bi-modal home ranges with frequent travel from interior terrace areas to roadside areas, whereas possum 30 displayed more generalised movements centred on the roadside. The remaining possums, 20, 36 and 46, were located in central terrace areas (Figure 3.5, Figure 3.11 and Figure 3.14). Possum 20 made use of the clear banks either side of the central creek for occasional long distance travel forays, but in general exhibited a uni-modal home range centred on the central creek. Possums 36 and 46 displayed much more generalised home ranges and very little evidence for favoured areas. Possum 46 was the most mobile of the sample possums, ranging widely across the southern terrace, yet making very little use of roadside areas.

3.3.4 Den sites

Specific den sites were infrequently identified, but when they were they typically occurred in the roots of mature *Nothofagus* trees, tree hollows and rotten stumps. Possums utilised multiple den sites throughout their home ranges and there was

evidence to suggest that these dens were sometimes grouped in favoured den areas (Figure 3.16).

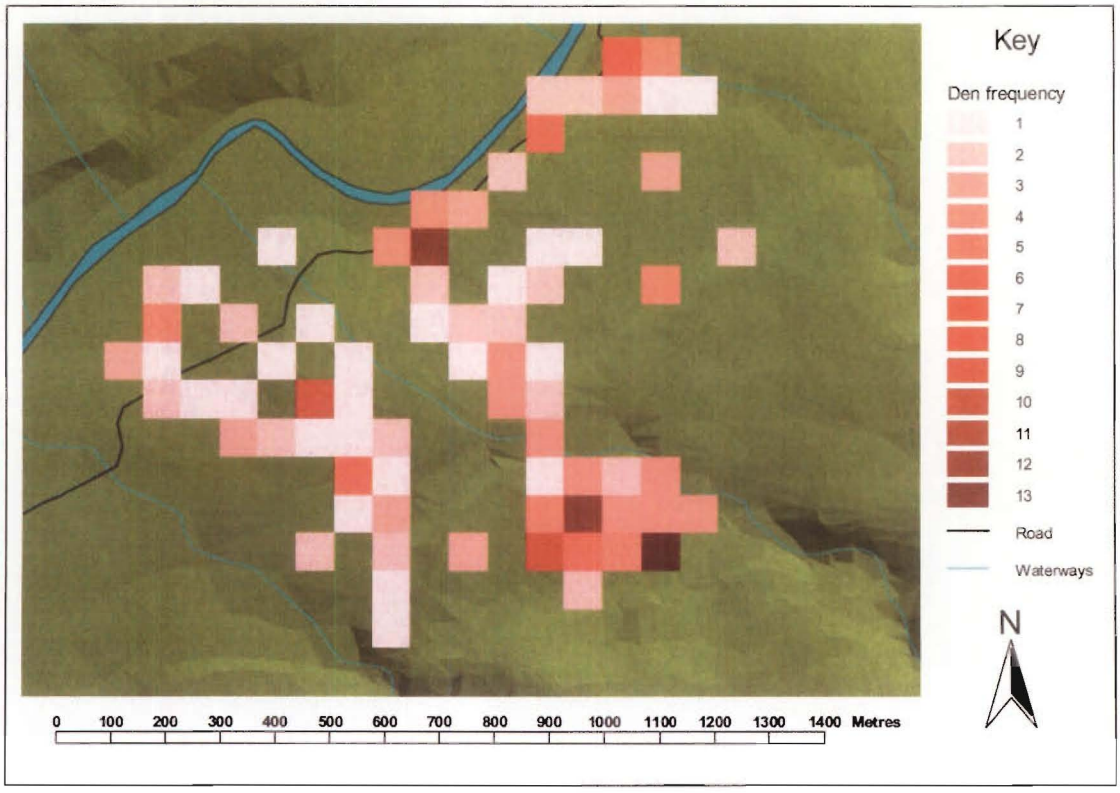

Figure 3.16: Aggregated locations of den sites for all sample possums.

3.4 Discussion

The activity patterns of the possums at the Palmer Road site were similar to those of possums in forested environments throughout New Zealand. Home ranges varied greatly in stability and size, overlapped considerably, often had multiple activity centres, and extreme movements within home ranges were sporadic.

3.4.1 Home range

The differences in home range size obtained with the MCP and kernel method are readily apparent; the MCP method produced both the smallest and largest home ranges. Wide-ranging possums often had many widely spaced peripheral points surrounding areas that were likely seldom or never utilised. This probably led to MCPs that represented areas larger than those truly used, which is a well-recognised

shortcoming of this method (Harris *et al.*, 1990). Although this situation is unlikely when MCPs were applied to sessile possums, it could be argued that the MCP method is limited by the locations of the outermost points and ignores the fact that possums may have utilised areas outside of this range when they were not being radio-tracked. As such, it could be said that the MCP method underestimated the true size of home range for sessile possums, as even small undetected movements would have been relatively influential on home range size when compared to similar movements for already large home ranges. The kernel method is not affected in this way and, as such, likely provides a better estimate of range size than the MCP method.

Comparisons with home ranges obtained from other studies must be made with caution because the method of data collection, choice of home range estimator and user defined settings severely influence home range size (Worton, 1989; Harris *et al.*, 1990; Gallerani-Lawson and Rodgers, 1997; Seaman *et al.*, 1998). Bearing this in mind, it appears that possum home ranges obtained in this study are larger than those found in continuous forested areas in New Zealand, but are smaller than those found in some forest/pasture or scrub/pasture complexes (Table 3.5).

It has been suggested that possum home range size and shape is influenced by habitat, density relative to carrying capacity, and absolute density (Cowan and Clout, 2000). The influence of density is twofold; density dictates the frequency of social interaction and also the competition for resources. Because possum home ranges overlap extensively (Cowan and Clout, 2000), evidence for the influence of social interaction, in the form of dominance, on home range size and shape is weak at best. Breeding behaviour, on the other hand, may be more influential as males seek out mates (Sutherland, 1996). Nevertheless, because breeding behaviour is only likely to be exhibited for a short period of time, habitat characteristics are likely the primary drivers of possum home range size and shape.

The relatively large home ranges observed in this study can be explained by the food exploitation hypothesis (FEH), which states that home range size is dependent on the distribution and quality of resources in an animal's environment (Larter and Gates, 1994).

Table 3.5: Summary of home range sizes and range lengths obtained from some studies of possums in New Zealand (sourced from Cowan (2000)). The table is ordered by decreasing home range size or range length if home range areas were not given. The type column refers to the study method type (R = radio-tracking, T = trapping and A = a mixture of R, T and spotlighting). The figures obtained in this study are given for MCP calculation, as this is the most commonly used method for possum home range estimation in New Zealand.

Vegetation type	Home range area (ha)		Home range length (m)		Type
	male	female	male	female	
Pasture/scrub/ Willows	29.9 (10.4-61.3)	31.0 (2.2-105.2)	883 (480-1370)	784 (250-1650)	R
Pasture/Podocarp-mixed broadleaf forest	24.6 (2.5-65.0)	18.3 (4.2-45.8)	880	820	R
This study	**10.0 (4.4-21.5)**	**5.5 (3.1-10.8)**	**456 (310-629)**	**456 (267-754)**	**R**
Nothofagus forest			529	390	T
Pasture/remnant forest	5.6	1.7	544	292	R
Podocarp-mixed broadleaf forest	3.9 (3.1-4.8)	2.6 (2.2-3.0)	319 (278-360)	262 (260-263)	R
Modified forest, urban	1.5 (0.5-3.6)	2.7 (1.7-4.5)	260	210	T
Pasture/scrub/ remnant forest	3.1 (2.4-3.6)	0.9 (0.3-1.2)	435 (407-550)	295 (110-516)	T
Pine, scrub, forest areas	1.9	1.3	210	190	T
Pasture/scrub/ remnant forest	1.4 (0.1-8.8)	0.9 (0.05-2.32)	359 (100-652)	291 (66-616)	R
Pine plantation	1.4	1	280	220	T
Pine plantation	0.7 (0.4-0.8)	0.7 (0.2-1.4)	310	230	T
Podocarp-mixed broadleaf forest	0.8 (0.1-3.0)	0.5 (0.03-3.8)			A
Pine plantation			296-317	163-272	T

This suggests that possums in poorer quality habitat will need to travel further to obtain sufficient resources and will, subsequently, display larger home ranges. If the density of possum populations is taken to be an index of habitat quality, then *Nothofagus* forest represents some of the poorest quality habitat in New Zealand because it supports some of the lowest observed possum densities (Efford, 2000). The larger home ranges observed in this vegetation type is therefore a logical result of this.

Contradictory to the FEH, the largest possum home ranges in New Zealand are found in forest/pasture or scrub/pasture complexes (Cowan and Clout, 2000). Home ranges are larger than expected in these areas because individuals that den in the forest or scrub regularly travel long distances to feed on pasture species (Green, 1984; Green and Coleman, 1986). Nevertheless, it must be recognised that the large home ranges obtained in these heterogeneous environments may be an artefact of the shortcomings inherent with MCPs and similar methods of calculations outlined above. Possums in heterogeneous environments likely make frequent forays to and from feeding and denning areas without making extensive use of the areas in between (Jolly, 1976; Green and Coleman, 1986). As such, effective home ranges in these areas are likely to be smaller than the home range estimates obtained using MCPs or similar methods.

A further confounding aspect for the comparison of home ranges is the three-dimensional nature of possum home range, which is seldom if ever taken into consideration (Ward, 1978). Comparisons are hindered because different sites present different opportunities for exploitation of the vertical dimension. During telemetry at Palmer Road, possums were seldom observed climbing mature *Nothofagus* trees and there is reason to believe that a large amount of foraging was undertaken at low levels in the forest, as this was where the bulk of possum preferred species (*see review* Nugent *et al.*, 2000) was located. For this reason, home ranges within the Palmer Road study site were likely to be more two-dimensional than those in sites with abundant palatable canopy trees (e.g. podocarp-broadleaved forests).

The structure of home ranges within the study site varied considerably. Possums could be grouped dependent on whether they displayed singular or multiple activity centres. It is likely that these distributions reflect the distribution and quality of food within the study site. Possums that consistently and intensely used only one area

within their home range, likely did so as a result of preferential foraging in areas containing high density of food. In contrast, possums in low quality areas were more likely to have invested energy in searching for more widely distributed food as is predicted by the FEH. However, despite the lack of detection of any demographic correlates of home range size, the effect of inherent individual variability on home range size and shape cannot be discounted.

Home range size was found to vary significantly between two bi-monthly groups only, where it was significantly smaller in the winter months (July/September) when compared to the autumn months (March/May). Under the FEH this change in home range size could be assumed to be related to a change in foraging strategy. This may either arise from a switch in diet or a change in the distribution or quality of diet constituents. As possum diet has been shown to be highly seasonal in other forest types (Harvie, 1973; Fitzgerald, 1976; Fitzgerald, 1978; Warburton, 1978; Coleman *et al.*, 1985; Cowan and Moeed, 1987; Cowan, 1990b; Owen and Norton, 1995; Allen *et al.*, 1997; Cochrane *et al.*, 2003), the former is more likely. It is possible that because possums consume more concentrated food sources in winter than they do in autumn (Chapter 5), they need to travel less distance in order to obtain sufficient sustenance.

Nevertheless, evidence to suggest great variation in bi-monthly group ranges was absent. Indeed, there was a high degree of shared area between the different temporal scales, which suggests that possums did not have widely different range locations during different seasons. Of the possums that survived the duration of the study, possums 44, 48 and 22, located in the upper section of the central creek, and possum 24, located on the roadside, displayed the greatest site fidelity, with the greatest shared home range area across temporal scales. In contrast, possums 36 and 46, located within the southern terrace, displayed the most variable ranging behaviour, with the least shared home range area across spatial scales. It is likely that these observed differences in site fidelity are related to the spatiotemporal distribution of resource quality within the general locality of individual possums.

3.4.2 Range lengths

Concurrent with home range size, annual range lengths within the study site were large on average for forested environments, yet smaller than those reported for the forest/pasture or scrub/pasture habitats (Table 3.5). In particular, the annual range lengths observed for this study are very similar to those reported by Clout and Gaze (1984) in a similar *Nothofagus* forest, although it must be recognised that they were derived from trapping data, which is a method that has been shown to underestimate true range length (Ward, 1984).

Nightly movements of over 800 m have been observed in several studies (Jolly, 1976; Ward, 1978; Clout and Gaze, 1984; Green and Coleman, 1986; Brockie *et al.*, 1987). It is generally assumed that these movements are motivated by acquisition of resources. Influential factors may include discrete sites containing abundant seasonally-available food (Jolly, 1976; Ward, 1978) or forests with extensive altitudinal stratification (Green and Coleman, 1986). As such, the lack of movements of over 800 m in this study suggests that the dispersion of resources and the relative desirability of those resources were not variable enough to prompt possums to make long forays to exploit them. Other studies have indicated that possums seldom travel far to feed on palatable food sources when there are other alternative food sources available (Thomas *et al.*, 1984). It is unlikely that possums in continuously forested vegetation types travel distances greater than 800 m, unless food within the forest is generally poor and patches of highly palatable food are present, or the forest has a high degree of altitudinal stratification.

3.5 Conclusions

The radio-tracked possums within the study site exhibited high mobility when compared to possums studied in other continuously forested sites within New Zealand, yet low mobility when compared to possums inhabiting some pastoral/forest complexes or forests bordering pasture. Extreme movements were rare and change in home range size was limited to smaller range sizes in winter when compared to autumn. In general, possums within the study site displayed high site fidelity. Similar to possums studied elsewhere, home ranges overlapped extensively and high

variability was displayed with respect to home range size and shape between individuals.

The home ranges derived in this chapter are related to the vegetation parameters described in Chapter 4 within Chapter 5 in order to identify potential motivations for movement parameters. In addition, the management implications of the home range sizes and range lengths observed in this study are outlined in Chapter 6.

Chapter 4: Vegetation Heterogeneity

4.1 Introduction

The characteristics of the vegetation within forested ecosystems influences both the biotic and abiotic environment therein (Kitteredge, 1973; Purves *et al.*, 1995). It follows that, as behaviour is the expression of the combined effects of an animal's genotype and the environment (Foster and Endler, 1999), the vegetation characteristics of a forest will affect the behaviour of animals inhabiting it.

Herbivores respond to vegetation characteristics in order to satisfy requirements for nutrition and shelter (Purves *et al.*, 1995; Pough *et al.*, 1996). Specifically, vegetation heterogeneity has the greatest influence, as the distribution of resources will dictate how a herbivore forages (Laca and Demment, 1991; Illius and Gordon, 1993). Important components of heterogeneity include structure, species diversity, abundance, spatial relatedness, and phenology. Foraging responses to this heterogeneity include seasonality of diet (Stephens and Krebs, 1986), avoidance of predators, and shelter from the environment (Pough *et al.*, 1996).

Because of this influence on herbivore foraging, an understanding of the floristic heterogeneity that a herbivore experiences should be considered a prerequisite for understanding the motivations behind that herbivore's behaviour (Laca and Demment, 1991). Although it must be recognised that learning and memory modify this behaviour (Drickamer *et al.*, 1996).

Upon first examination, the vegetation at the site studied here appears to have low heterogeneity when compared to many other New Zealand forest types (Wardle, 1991). As with all ecosystems, perceived heterogeneity is relative to the scale at which it is observed (Kotliar and Wiens, 1990; Levin, 1992; Begon *et al.*, 1996). Imposing human perceptions of heterogeneity on wildlife research is questionable because, as Klopfer (1985) put it, "No other species sees the world as we do, and without insight into how another's perceptions are formed, our correlations are likely to be spurious". Possums are much smaller and less mobile than humans are; it is likely that they operate at different spatiotemporal scales and perceive their

environment differently. As such, the likelihood of obtaining robust inferences from observed interaction between possums and their environment is dependent on analysis of vegetation heterogeneity within the study site proceeding at scales meaningful to possums.

Studies on possum diet have indicated that New Zealand species within the genus *Nothofagus* are relatively unpreferred by possums (Owen and Norton, 1995; Sellar, 1998; Cochrane and Norton, 2000; Cochrane *et al.*, 2003; *but see* Sweetapple, 2003). This provides an interesting contrast between *Nothofagus* forests and commonly studied podocarp/angiosperm and *Metrosideros umbellata* / *Weinmannia racemosa* forests where palatable species comprise a significant component of the canopy (Fitzgerald, 1976; Fitzgerald and Wardle, 1979; Coleman *et al.*, 1985; Nugent *et al.*, 1997). As such, the distribution of palatable species within *Nothofagus* forest is likely to be more heterogeneous than that of other forest types because palatable species within *Nothofagus* forests are most likely to occur in open sites. Previous diet assessment of possums resident in the study area indicated that seral species, such as *Aristotelia serrata* and *Fucshia excorticata*, comprised a disproportionately large proportion of the overall diet (Cochrane *et al.*, 2003). The growth strategies of these species predispose them to high abundance in open and disturbed areas (Wardle, 1991), which are spatially patchy in the forest. Similarly, the dominance of *Nothofagus* species within the study forest likely dictates the distribution of other palatable species such as *W. racemosa* and *Muehlenbeckia australis*. Such heterogeneity is likely to have implications for possum foraging within the study site.

The objectives of this chapter are to:

- Analyse and describe the spatial and temporal heterogeneity of the vegetation within the study site in terms of relative abundance, distribution and phenology of constituents;

- Classify the vegetation into vegetation types to be used for subsequent habitat selection analyses.

4.2 Methods

4.2.1 Vegetation survey

In order to maintain the grain of scale throughout the study, the 0.5 ha cells used to record radio-tracked possum location were also used as the unit of vegetation assessment. Cells were selected for vegetation assessment if they had experienced use by possums at any time during the radio-tracking period. Cells that were unused by possums were not assessed for several reasons: it is difficult to determine which unused cells should be included and which excluded, whereas differentiating between used and unused is much more pragmatic; modelling of vegetation attributes in Chapter 5 does not require a distinction between used and unused, simply more used and less used is sufficient; and time and labour constraints prevented a more comprehensive survey.

Navigation to cells and cell boundaries was achieved with the use of a mobile global positioning system (GPS) unit (Leica GS50™) with waypoints representing cell locations. The Leica GS50™ utilises an algorithm that facilitates effective tracking of satellites through moderately dense forest canopies.

Vegetation composition and structure for each cell was assessed using an adaptation of the recce procedure (Allen and McLennan, 1983). Cover abundance scores for established vascular plant species were recorded; cover abundance scores of 1, 2, 3, 4, 5, 6 and 7 related to cover abundance classes of <1, 1-5, 6-10, 11-25, 26-50, 51-75 and 76-100 %, respectively. Cover abundance was apportioned into four tiers: ground, shrub, subcanopy and canopy. The heights of these tiers varied and were recorded separately for each cell. Where obvious areas of discontinuity were apparent, such as a sudden change in slope or break in the canopy, cells were subdivided to encapsulate this heterogeneity. Site factors were not recorded due to their variability within each cell. Correction of cell area for slope was not warranted because slope was generally low and consistent throughout the majority of the study site. The recce method is fast and efficient (Wardle, 1986), and is widely used for studies of forest ecology in New Zealand.

Temporal variability of vegetation was assessed with phenological observations made on previously identified palatable species (Cochrane *et al.*, 2003) in conjunction with radio-telemetry outings. These species consisted of trees, *A. serrata*, *F. excorticata* and *W. racemosa*, a liane, *M. australis*, and a herb, *Trifolium repens*. Events such as flowering, fruiting and the production of new growth were recorded on a five-point scale of abundance: absent, sparse, low, moderate and abundant. Observations were not made on individual plants *per se*; rather, they were made on groups of plants along regularly traversed pathways used for radio-tracking.

4.2.2 Vegetation community classification

Formal classification of vegetation was performed using the TWINSPAN (Two-Way Indicator Species Analysis) classification programme within the PC-RECCE package (Hall, 1992). TWINSPAN uses a polythetic divisive method to split groups using differential species as indicators (Hill, 1979). The data format utilised by TWINSPAN is that of a species importance matrix, which is comprised of singular importance values for each species in each cell. The transformation of survey data into importance value data was performed by the programme RECINT within PC-RECCE. Within this program, mean cover abundances were multiplied by the tier span and were then summed across tiers to achieve singular importance values. In notational form this process is given as:

$$I_i = \sum_{j=1}^{4} C_{ij} H_j \qquad \textbf{Equation 4.1}$$

where I_i is the importance value of species i, C_{ij} is the mean cover abundance of species i in tier j, and H_j is the height of tier j.

Cover abundance is recognised as a positive correlate of biomass (Mueller-Dombois and Ellenberg, 1974; Chiarucci *et al.*, 1999); therefore, species importance values can also be taken as an index of biomass or density.

Classification using the default settings in TWINSPAN generates potential vegetation types based on the variability of all species. This neutral weighting of species defies a study-organism-specific approach. A possum specific approach was adopted and was based on the assumption that possums were far more likely to respond to palatable

species distribution and abundance than to unpreferred species distribution and abundance. Specifically, this approach involved decreasing the classification potential of *Nothofagus* species in TWINSPAN analysis. These unpreferred species dominate the study site in terms of frequency of occurrence and cover abundance, and are, therefore, likely to dominate or drive classification analysis whilst providing low potential for influence over possum behaviour within the forest. Suppression of their dominance within the data set was achieved by using a natural log transformation of importance values for all species. This has a convergent effect on the relative importance of species. The decreased influence of *Nothofagus* species in the analysis is likely to highlight the heterogeneity with respect to other, more preferred, species within the forest. It must be recognised that *Nothofagus* species may have exerted unforeseen influence on possum behaviour, but because these species were present throughout the study site, such an influence was unlikely to be highly heterogeneous.

Examination of the species importance value matrix indicated that abundant species were not adequately represented by the default pseudospecies cut levels proposed in TWINSPAN, which were accordingly reset to 0, 1, 2, 3 and 4. These cut levels were chosen because they provided pseudospecies group numbers of roughly equivalent size.

The TWINSPAN classification system requires careful interpretation of the output to determine the appropriate level of divisions for each hierarchical 'arm'. This decision is facilitated by examination of division eigenvalues and use of other analysis techniques such as ordination. Ordination is primarily a descriptive tool, which allows investigation into the structure of vegetational variation (Dale, 1975; Gauch and Wentworth, 1976), and identification of dominant environmental gradients (Mueller-Dombois and Ellenberg, 1974; Orloci, 1978; Whitaker, 1978). When used in conjunction with specific classification methods, ordination can provide useful verification of vegetation communities (Orloci, 1978; Whitaker, 1978). Ordinations were performed using detrended correspondence analysis (DCA) (Hill and Gauch, 1980) in CANOCO (ter Braak and Smilauer, 1998) with down-weighting of rare species. Down-weighting was chosen to reduce the influence of rare species within the analysis. Such species may be small, ephemeral or difficult to detect, which likely resulted in a failure to detect them in many cells and, therefore, a bias in the data set.

Down-weighting of rare species should not be seen as contradictory to the log-transformation approach in this study, as down-weighting rare species is done on frequency criteria, not abundance (ter Braak and Smilauer, 1998). Direct ordination methods were not applicable due to the lack of suitable environmental data for each cell. Given the subjective nature of classification it is advisable to limit divisions to broad groups in order to reduce the likelihood of obtaining vegetation types with high similarity. Furthermore, simplified classifications are more likely to yield robust results with habitat selection analysis (Aebischer *et al.*, 1993).

Species importance values were summarised by tiers and in total within each of the vegetation types. Summaries were also given for species richness and Shannon diversity index (SDI). SDI is not as sensitive to sample size within vegetation types as many diversity indices are and, consequently, provides a less biased estimate of species richness (Magurran, 1988). Furthermore, the SDI, as a heterogeneity index, incorporates a measure of evenness with species richness (Peet, 1974). The mean differences between these variables in each vegetation type were analysed using Tukey's studentised range (HSD) tests on pairwise comparisons. This test was also used to analyse differences in slope between vegetation types; slope was calculated for each cell using spatial analysis of 1:50,000 altitude contours (LINZ, 1999) in Arcview GIS 3.2a (ESRI, 2001).

Vegetation types were named using an adaptation of Atkinson's (1985) method. Species with greater than 60 % frequency of occurrence within specific vegetation types were used to name vegetation types. Species were listed in order of decreasing abundance, with no brackets indicating species importance across all tiers of greater than 50, and ( ) brackets indicating species importance across all tiers of between one and 50. A forward slash (/) was used to demarcate tier breaks, and species were listed in tiers within which they reached their maximum abundance. Hyphens were used to separate species within the same tier.

Once cells had been classified into vegetation types, GIS was used to represent them spatially. Classification of vegetation types was also extended into areas peripheral to the main study site using the vegetation types derived from TWINSPAN analysis. This was done by visiting peripheral areas and classifying then based on the

characteristics of the TWINSPAN derived vegetation types. The rationale for the classification of these peripheral areas is described in Chapter 5. Although the classification of these areas obviously represents a simplified approach, their importance in subsequent analysis is minimal because it is directly proportional to their distance from the location of the studied possums. Furthermore, the broad categories used to define vegetation types were unlikely to lead to significant error when classifying these areas. Attributes for all cells were entered into GIS to enable the production of maps defining the distribution of diversity, individual species importance scores and tier importance values. Aerial photographs were used to facilitate the classification of peripheral areas.

4.3 Results

During March 2003 vegetation was assessed for 166 cells, representing approximately 83 ha. Subdivision of cells to encapsulate heterogeneity yielded 276 assessed units in total. The simplified classification of peripheral areas was performed on a further 450 ha.

4.3.1 Species distributions

The distributions of species with greater than 60 % frequency and an overall importance value of greater than one for all cells can be seen in Figure 4.1 to Figure 4.5. Distributions are also given for *Weinmannia racemosa* (Figure 4.9), *Fuchsia excorticata* (Figure 4.11), *Aristotelia serrata* (Figure 4.10), *Trifolium repens* (Figure 4.12), *Rubus cissoides* (Figure 4.14) and *Muehlenbeckia australis* (Figure 4.13) because these species have been identified as highly palatable in other studies (Nugent *et al.*, 2000; Cochrane *et al.*, 2003).

N. fusca was clearly the most dominant species within the study site (Figure 4.1) and was present in high abundance throughout, except for roadside areas and windfall gaps. This species showed no distinct pattern of abundance, with high abundances occurring on all areas. *N. menziesii* was the next most dominant species within the study site, but, unlike *N. fusca*, its abundance showed a negative correlation with slope, being most abundant on flatter areas, which perhaps reflects the stability and

drainage properties of these sites (Figure 4.2). *Pseudowintera colorata* displayed a much more restricted distribution, occurring predominately along the margins of the central creek extending into the southern terrace (Figure 4.3). This area has been periodically flooded by the central creek and may have contained relatively recent, fertile soils. There were also numerous small creeks and seepages throughout this area. *Blechnum discolor* was clearly the most dominant component of the ground tier and was relatively ubiquitous except for steep areas and areas below the road (Figure 4.4). *Griselinia littoralis* was widespread throughout the study site, yet it occurred in the greatest abundance along a strip parallel to the road through the centre of the terrace (Figure 4.5). This distribution encapsulated a wide variety of substrate types and, therefore, may be driven primarily by competitive exclusion rather than by site requirements.

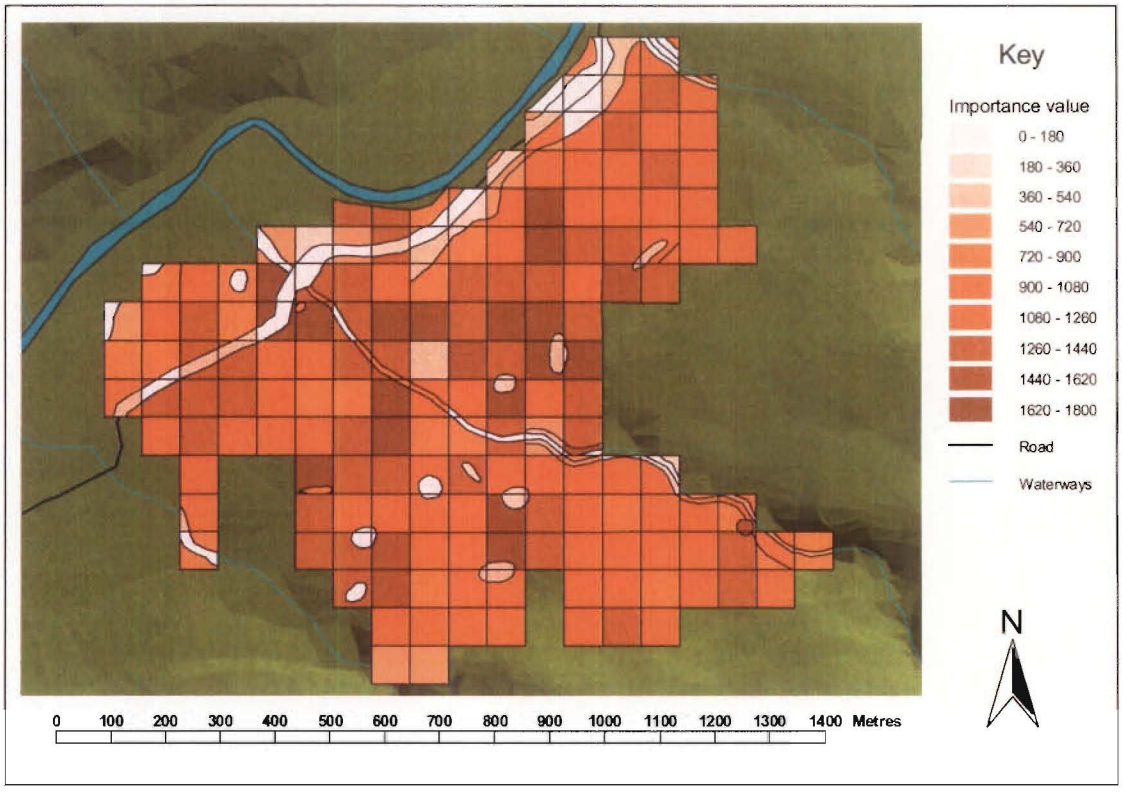

Figure 4.1: *Nothofagus fusca* abundance and distribution. The key scales on this and similar figures were derived by classifying the values within the ARCVIEW GIS legend editor. Apparent inconsistencies in the derived scales are rounding artefacts.

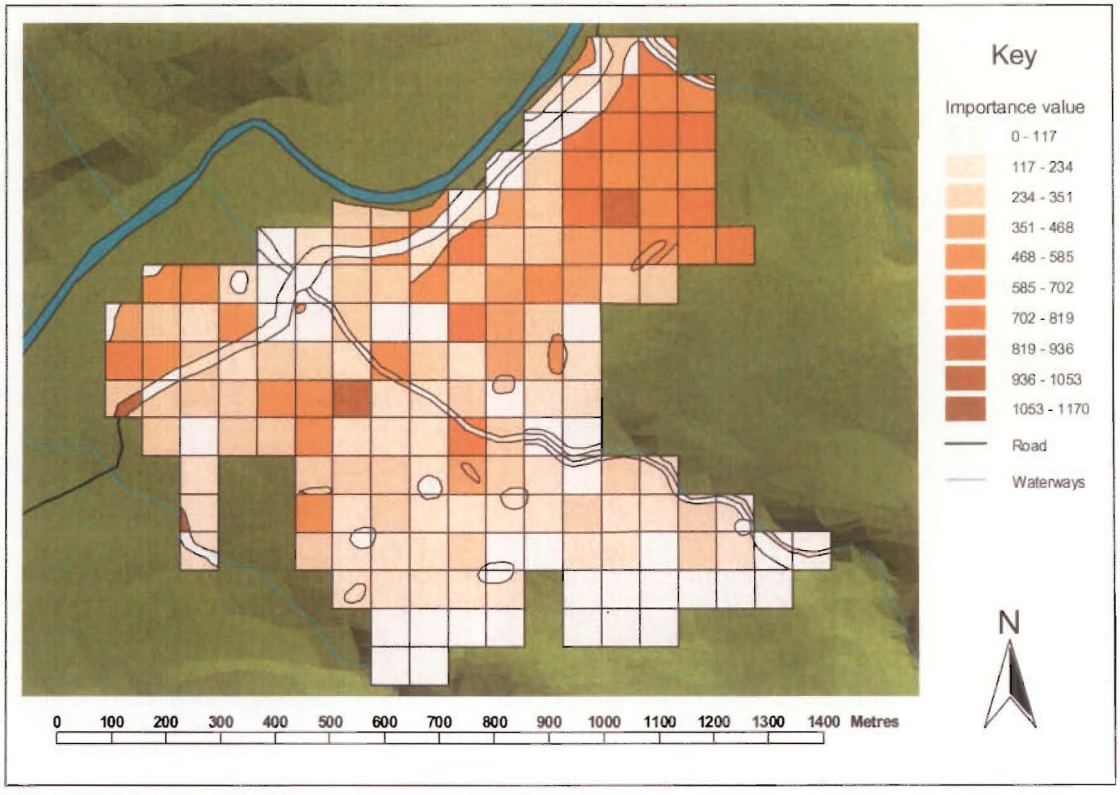

Figure 4.2: ***Nothofagus menziesii*** **abundance and distribution.**

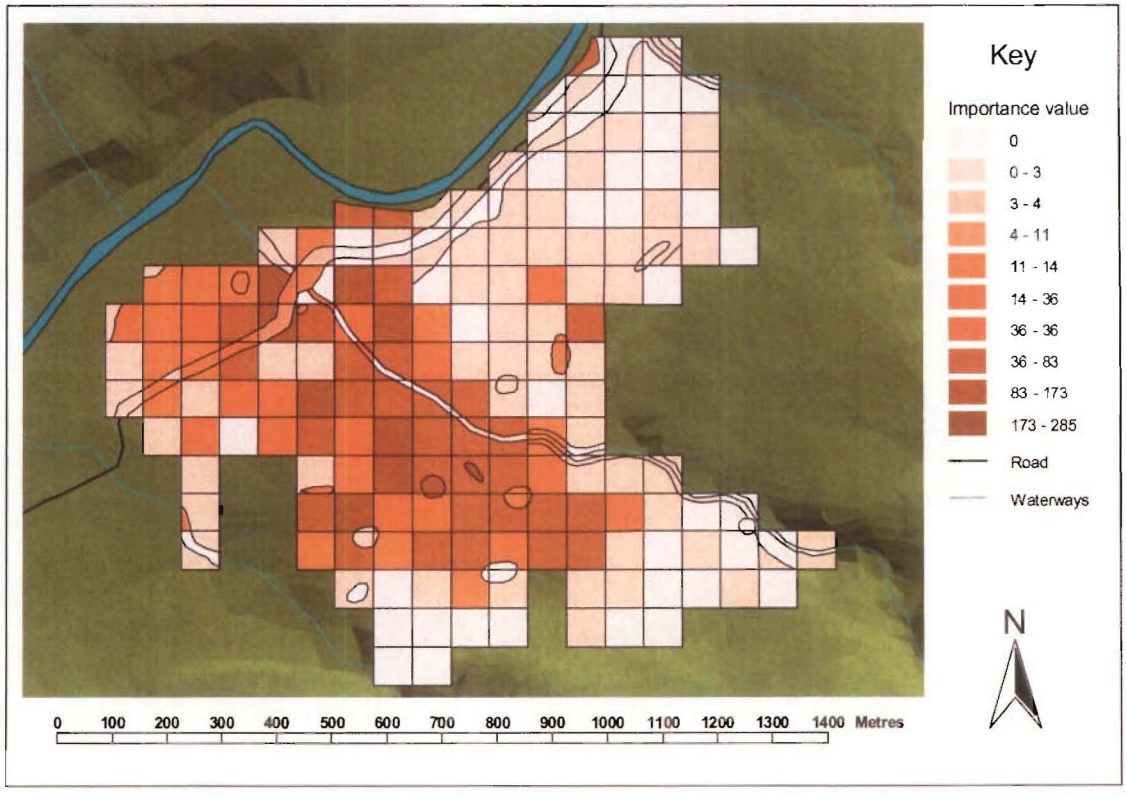

Figure 4.3: ***Pseudowintera colorata*** **abundance and distribution.**

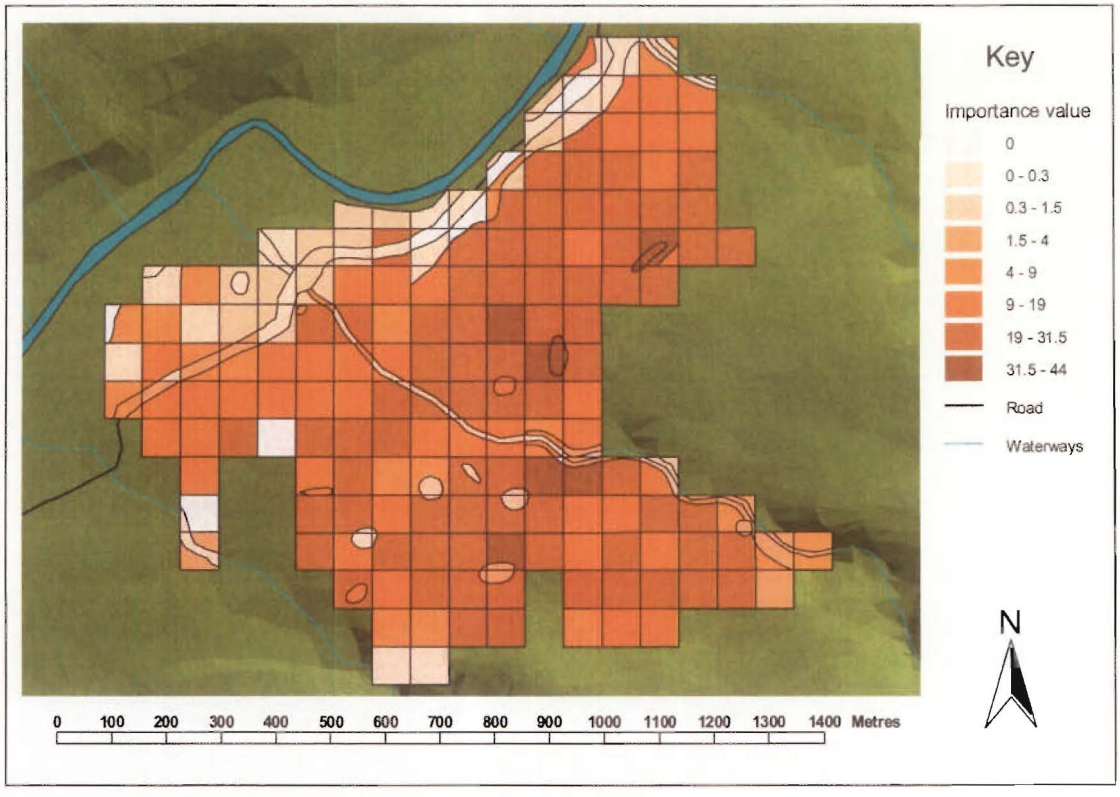

Figure 4.4: *Blechnum discolor* abundance and distribution.

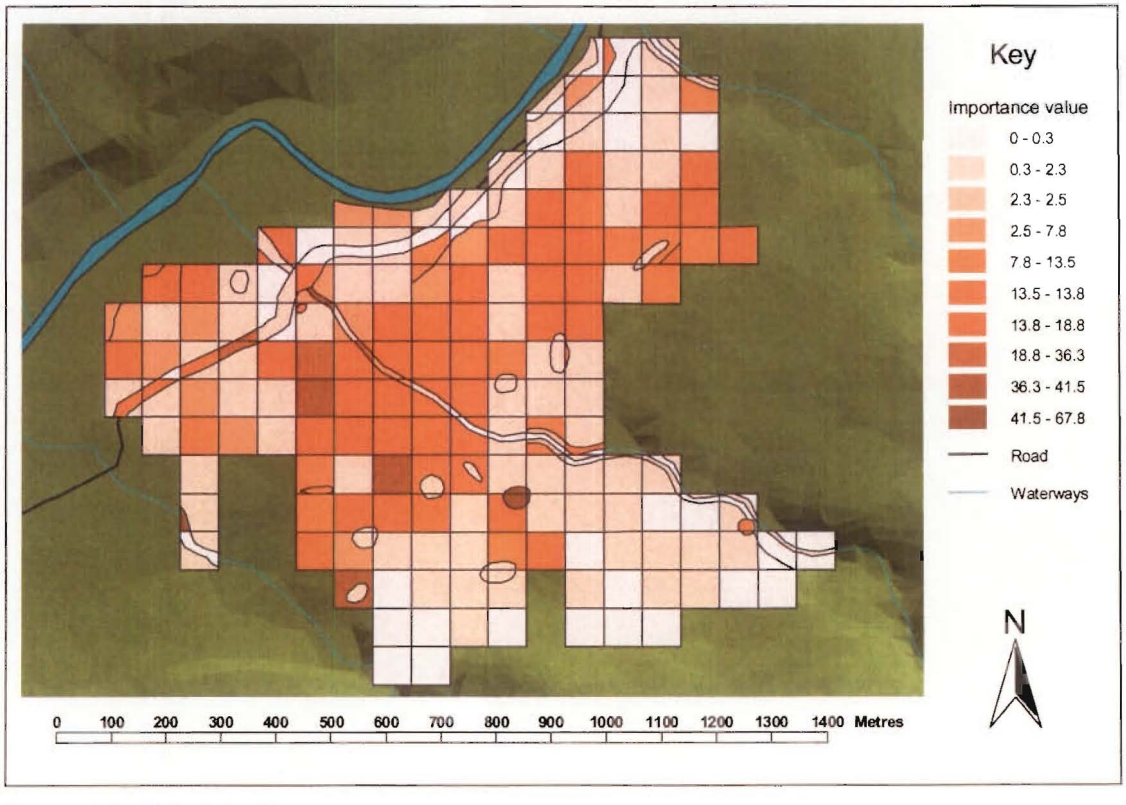

Figure 4.5: *Griselinia littoralis* abundance and distribution.

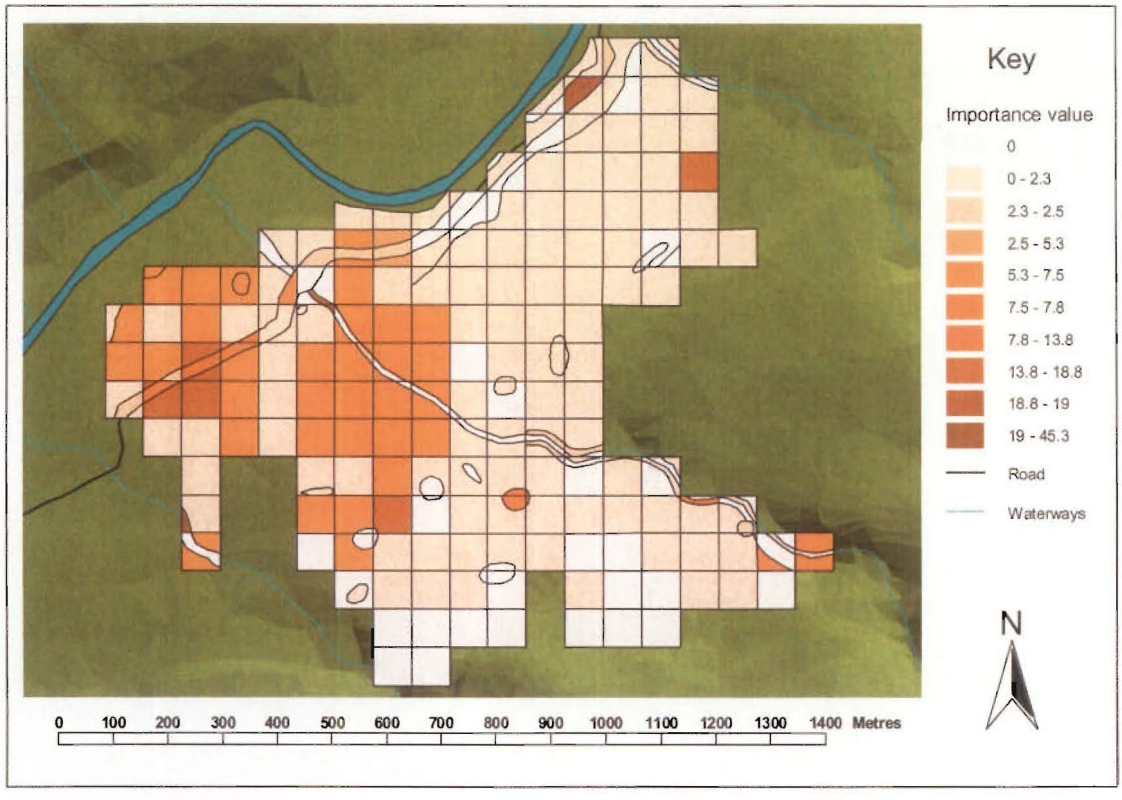

Figure 4.6: ***Pseudopanax crassifolius*** **abundance and distribution.**

Figure 4.7: ***Coprosma parviflora*** **abundance and distribution.**

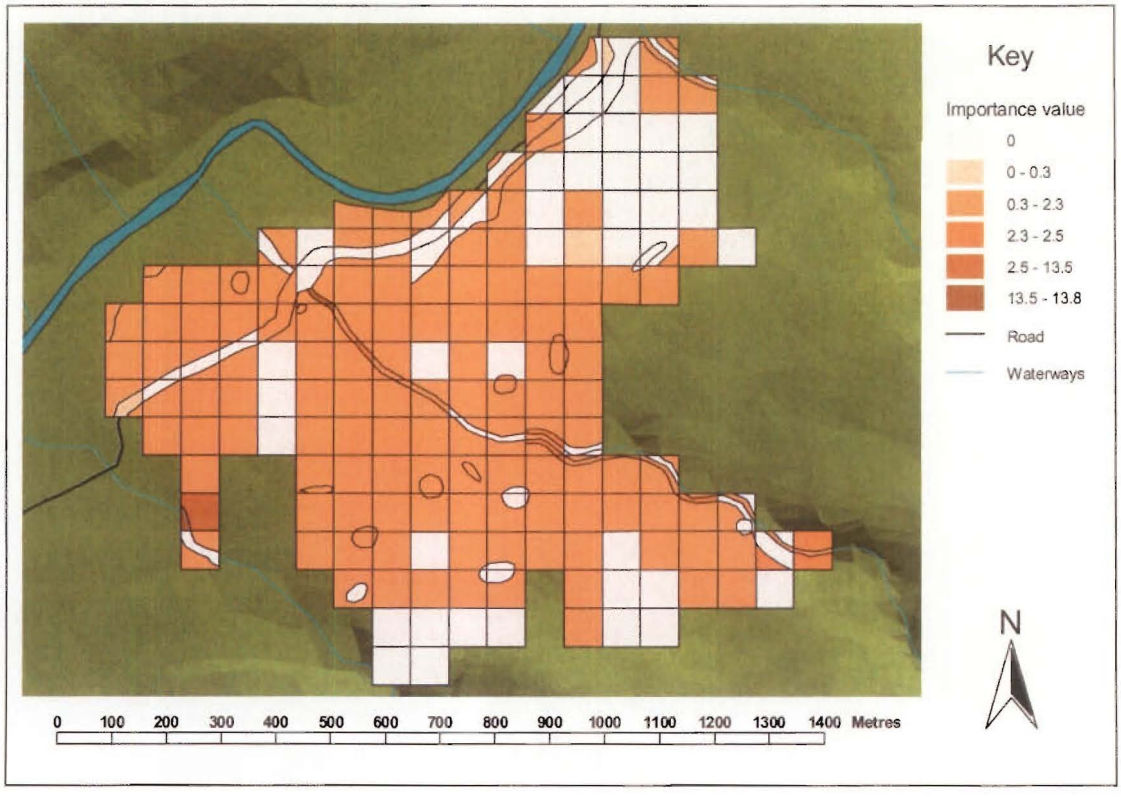

Figure 4.8: *Coprosma rhamnoides* abundance and distribution.

Pseudopanax crassifolius was a common species throughout the forest in low abundance, but was more abundant in western areas and along the roadside (Figure 4.6). *Coprosma parviflora* and *C. rhamnoides* were both widely distributed in low abundance and only reached high abundances in roadside and streamside areas (Figure 4.7 and Figure 4.8).

The roadside contained abundant palatable species; *A. serrata*, *F. excorticata* and *T. repens* occurred almost exclusively along it (Figure 4.10 and Figure 4.11) and *M. australis* and *R. cissoides* showed some preference toward it (Figure 4.13 and Figure 4.14). *W. racemosa*, in contrast, occurred in highest abundances on steep sites within the *Nothofagus* canopy (Figure 4.9). This included the lower hill slope and the escarpment area above the northern roadside. Of all the palatable species, the lianes, *M. australis* and *R. cissoides*, showed the greatest variability in distribution and abundance. This was likely a result of their ability to grow towards light gaps within the forest, in contrast to the shrub species which require more permanent light availability.

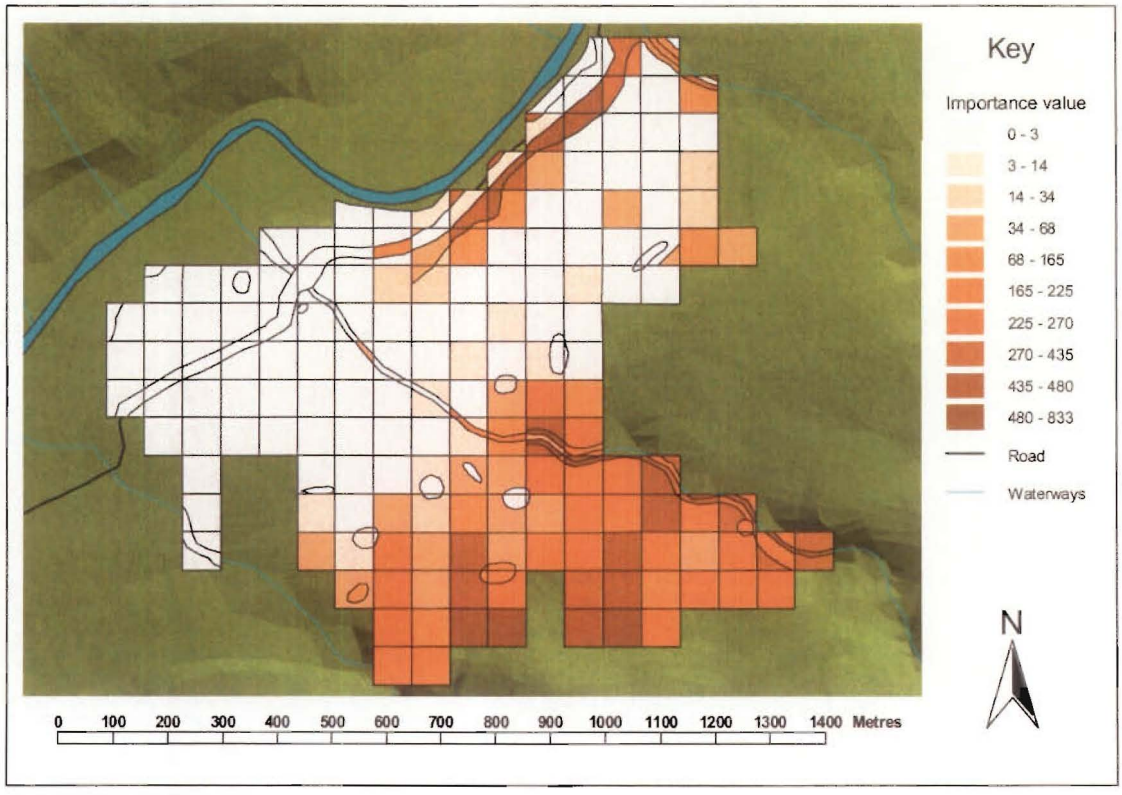

Figure 4.9: *Weinmannia racemosa* abundance and distribution.

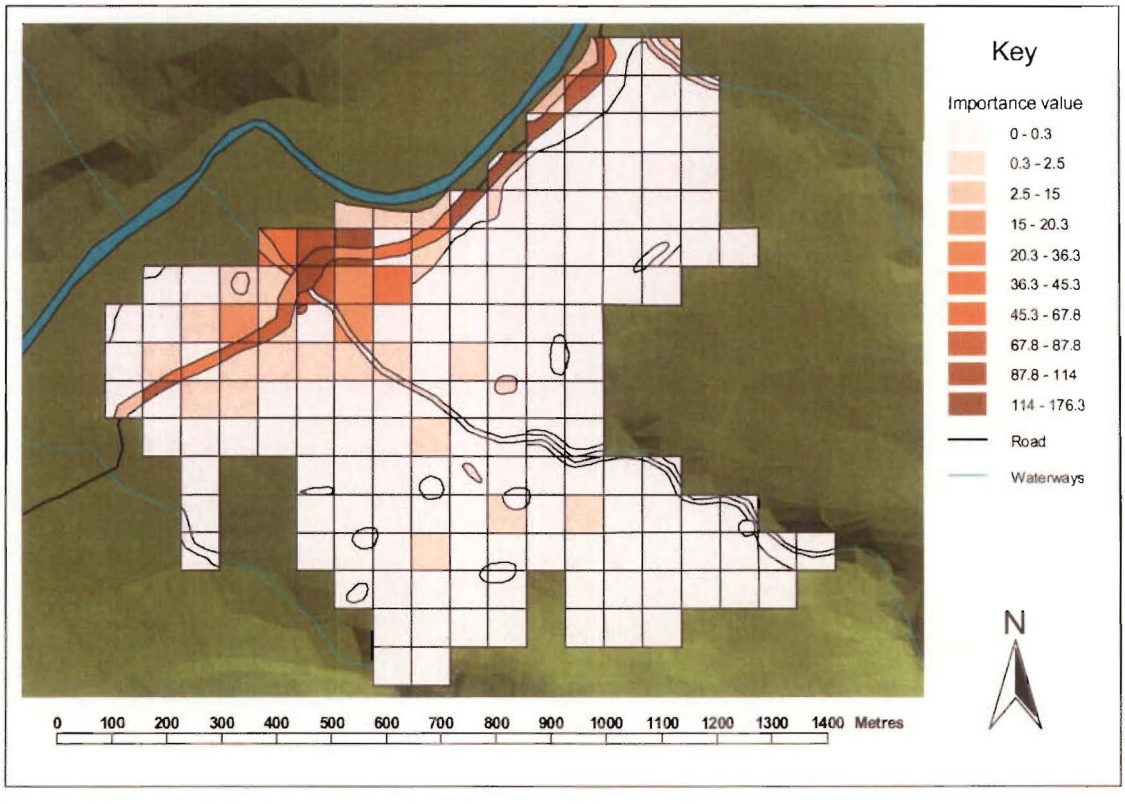

Figure 4.10: *Aristotelia serrata* abundance and distribution.

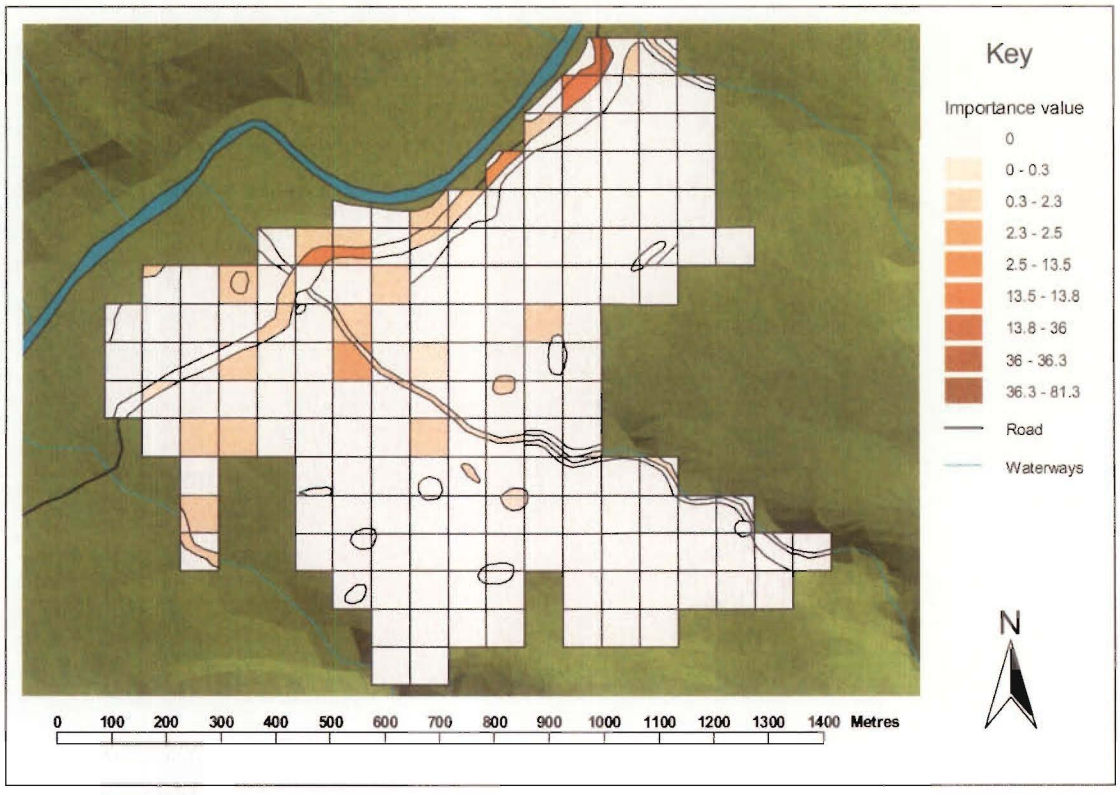

Figure 4.11: ***Fuchsia excorticata*** **abundance and distribution.**

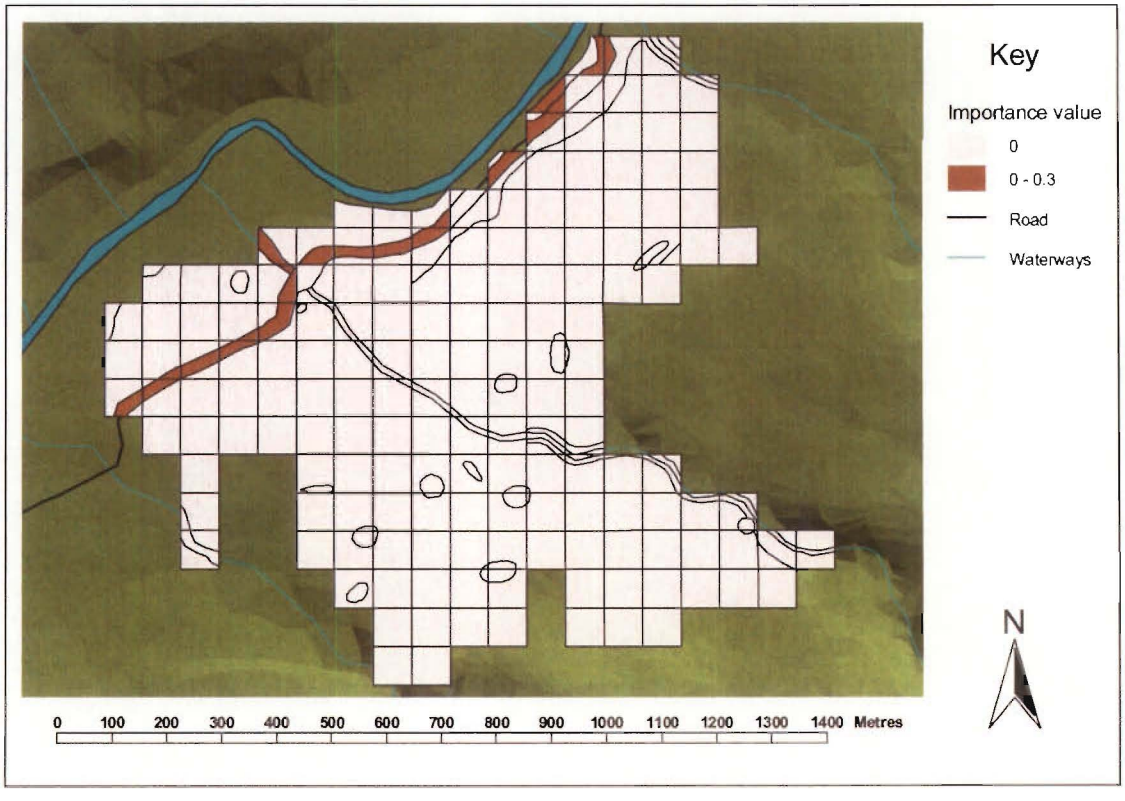

Figure 4.12: ***Trifolium repens*** **abundance and distribution.**

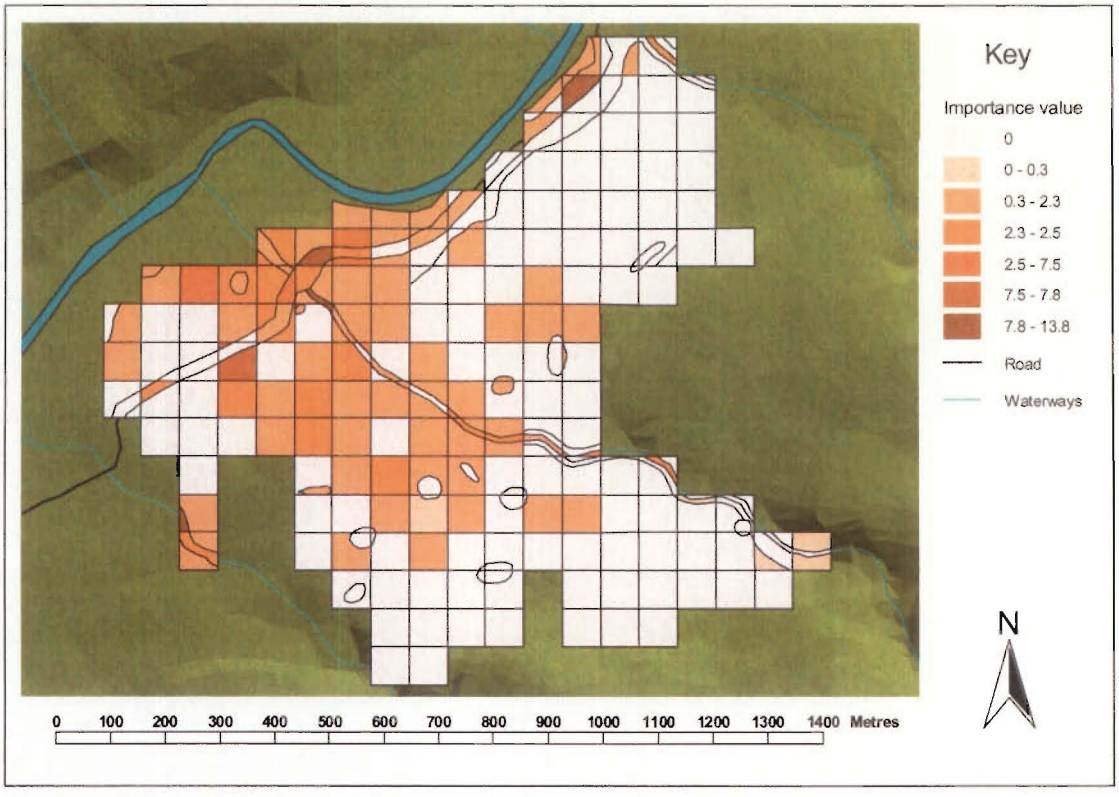

Figure 4.13: ***Muehlenbeckia australis*** **abundance and distribution.**

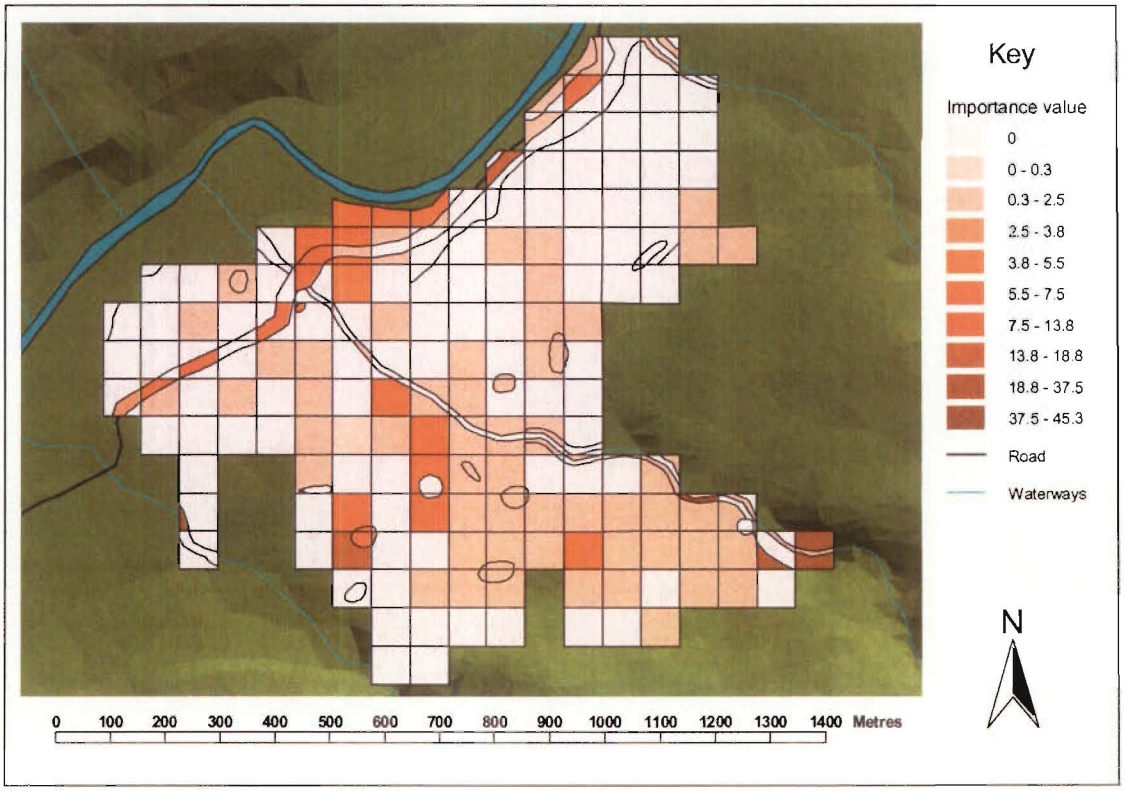

Figure 4.14: ***Rubus cissoides*** **abundance and distribution.**

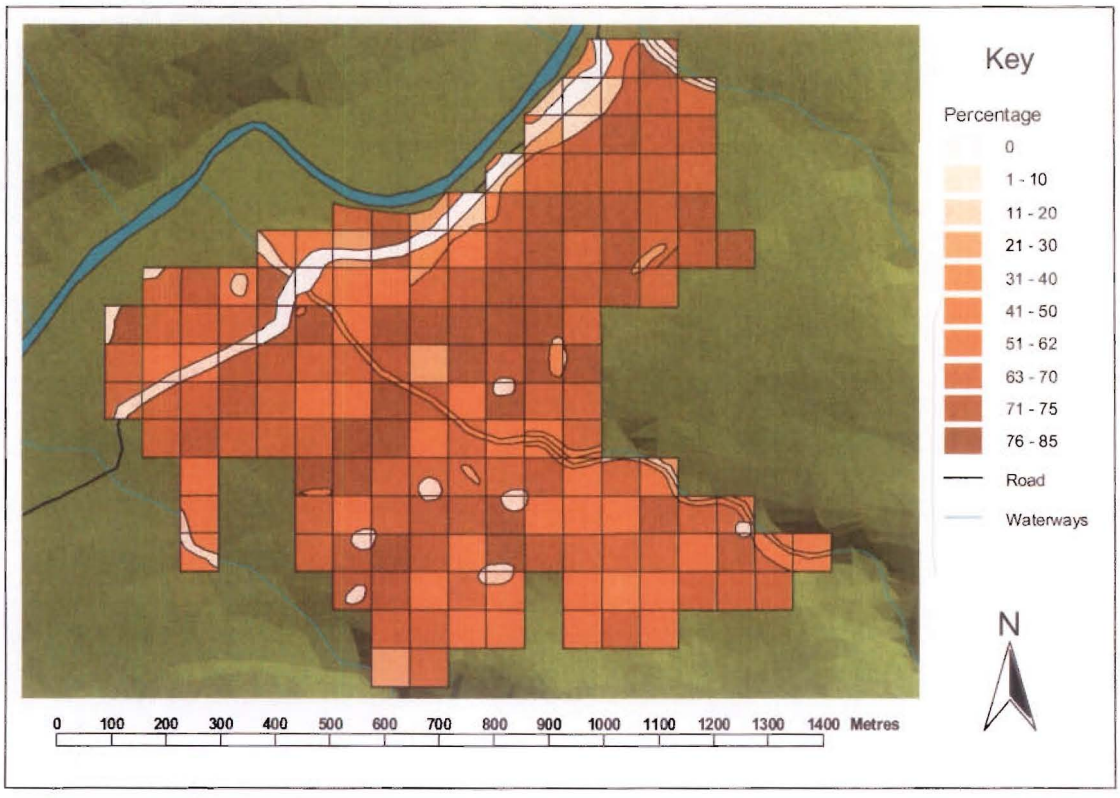

Figure 4.15: Canopy cover distribution.

The most continuous canopy occurred on the northern terrace, probably the least disturbed area of the study site in recent decades (Figure 4.15). Most large canopy gaps were located at the toe of the hillside on old debris fields; this suggests that the substrate in these areas made trees more prone to windthrow or earthquake damage, or that the topography of this area caused a wind funnelling effect, or a combination of both.

Vascular species diversity was highest in areas without significant canopy such as the roadside, swamp and windfall gaps (Figure 4.16). Indeed, SDI was found to be significantly negatively correlated with canopy cover (Pearson correlation coefficient = -0.72, $p<0.0001$). As such, diversity was lowest on the stable northern terrace and at the intersection between the central creek and the road.

It is apparent from the distributions of individual species, structural variables and diversity (Figure 4.1 to Figure 4.16) that the most pronounced discontinuities in the study site occur between the roadside, swamp and windfall gaps, and the forest.

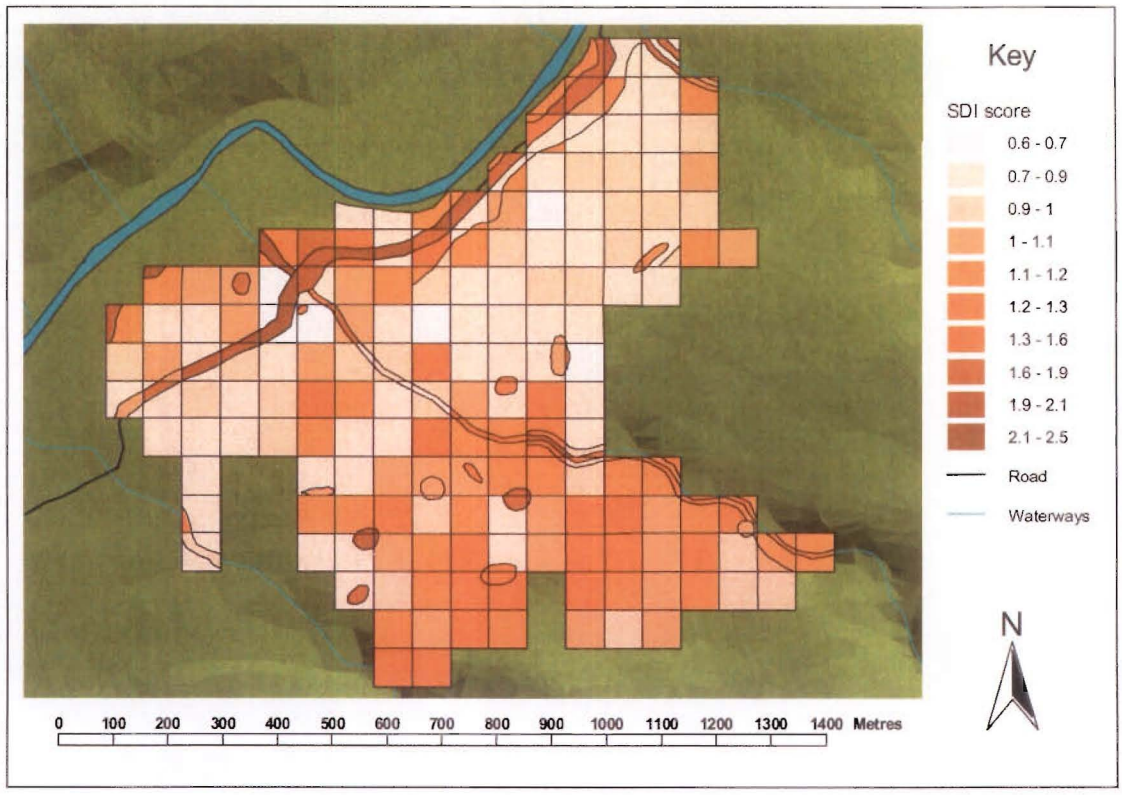

Figure 4.16: Distribution of SDI scores.

Correlations between species with frequencies of occurrence of greater than 25 % can be seen in Appendix 4. As was to be expected, most of the species were highly correlated either because they have similar requirements (positive correlation) or they have different requirements or one competitively excludes the other (negative correlation). The degree to which species are correlated gives a measure of their functional similarity. *N. fusca* and *N. menziesii* were most commonly negatively correlated with other species, indicating the exclusive effect of their dominance. However, *B. discolor*, *Neomyrtus pedunculata* and *Raukaua simplex* were significantly positively correlated with both *Nothofagus* species. Other species that were significantly correlated with individual *Nothofagus* species were *G. littoralis* and *Pseudopanax crassifolius* with *N. menziesii*, and *P. colorata* with *N. fusca*. These positive correlations suggest that these species are more resistant to the exclusive effect of *Nothofagus* species than are others, because the distribution of *Nothofagus* species appears to be primarily driven by disturbance, not site factors. Nevertheless, it must be recognised that the relationships between species are highly complex and, therefore, conclusions drawn from correlations between importance values must be conservative.

4.3.2 Structural distributions

The distribution of structural attributes within the surveyed region of the forest can be seen from Figure 4.17 to Figure 4.21. Canopy density was consistently high on the northern terrace, yet was more patchily distributed elsewhere. The lowest areas of canopy density occurred at the roadside, the swamp and in forest gaps. Subcanopy density (Figure 4.18) appeared to be high on steep areas of the site, probably a reflection of the abundance of *W. racemosa* at these sites. The least dense subcanopy occurred in western-most areas. The shrub tier (Figure 4.19) was most dense along the roadside and within canopy gaps, and was the most variable structural component. The ground tier (Figure 4.20) was much more evenly distributed with the highest density occurring in central areas.

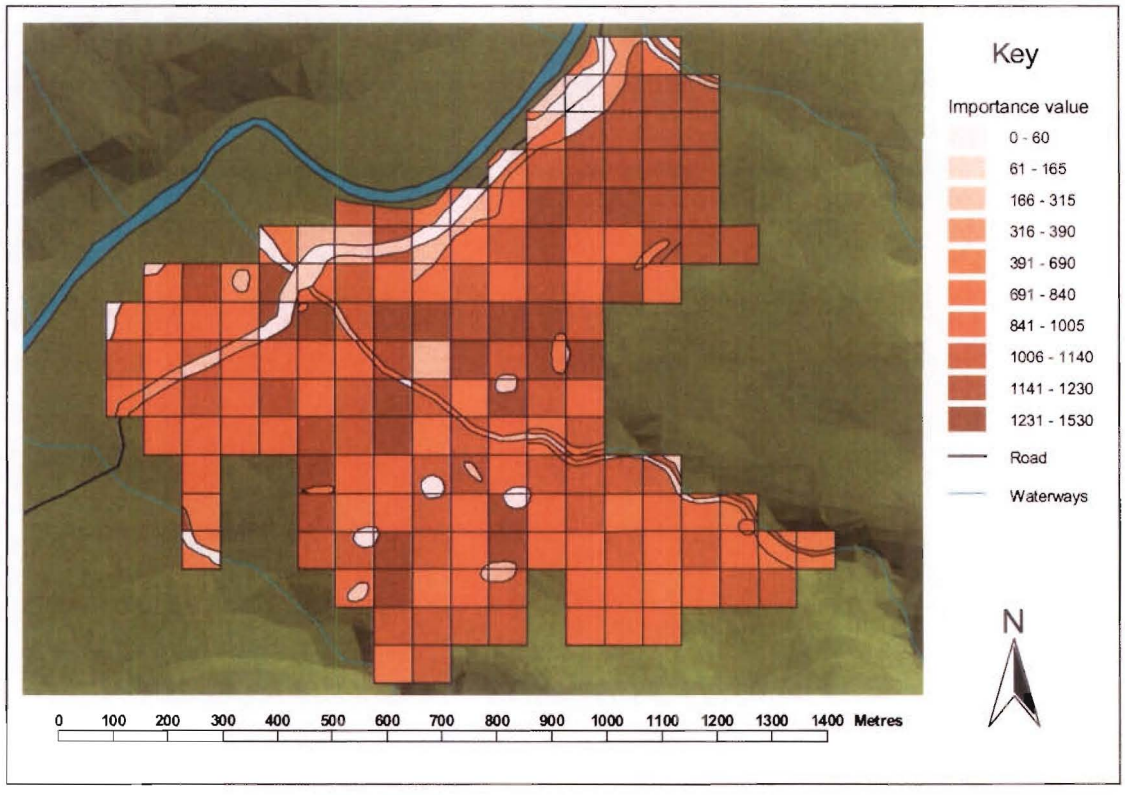

Figure 4.17: Distribution of canopy tier (tier one) importance value.

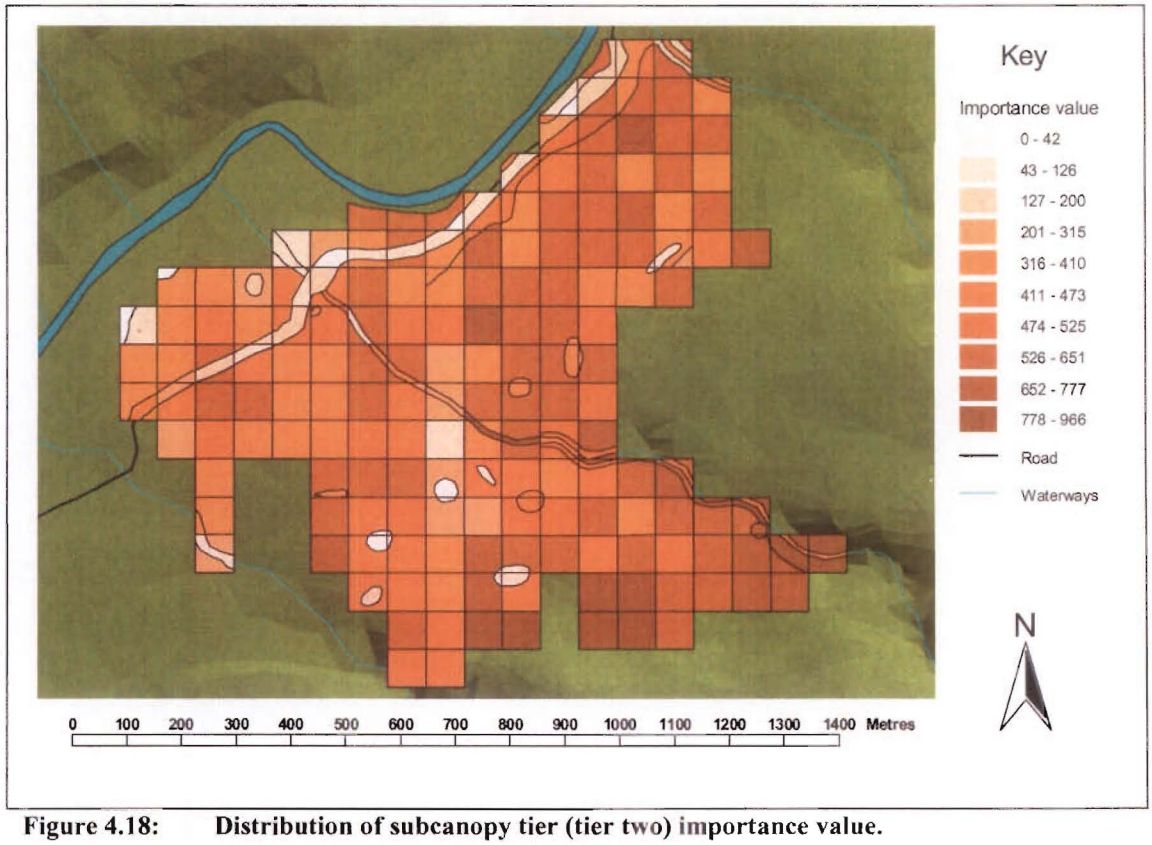

Figure 4.18: Distribution of subcanopy tier (tier two) importance value.

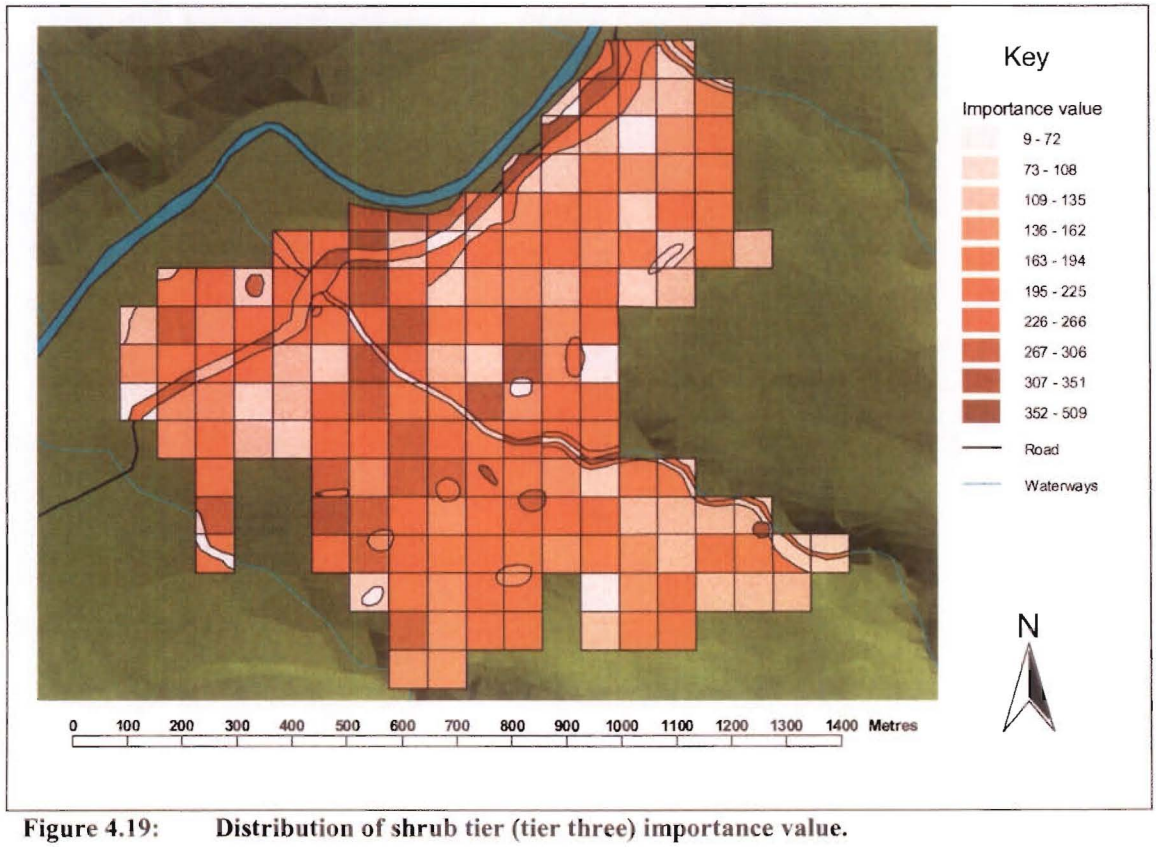

Figure 4.19: Distribution of shrub tier (tier three) importance value.

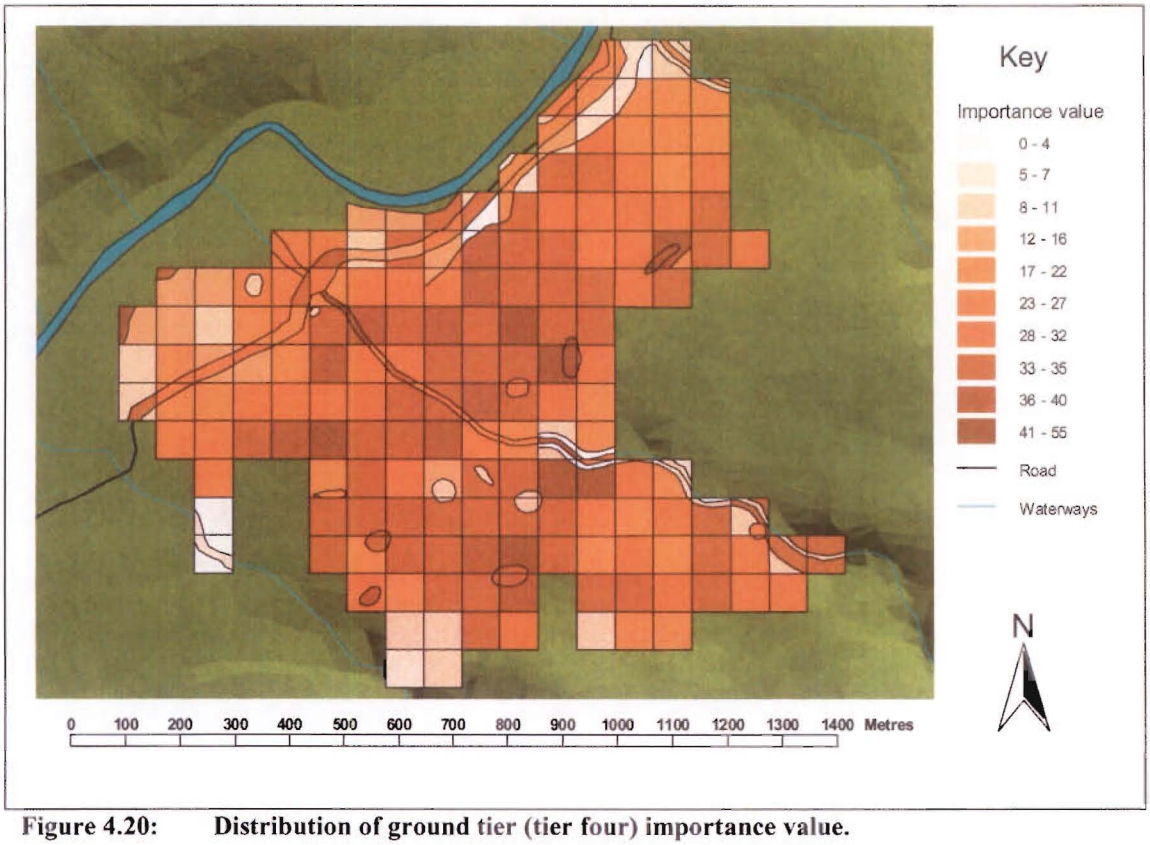

Figure 4.20: Distribution of ground tier (tier four) importance value.

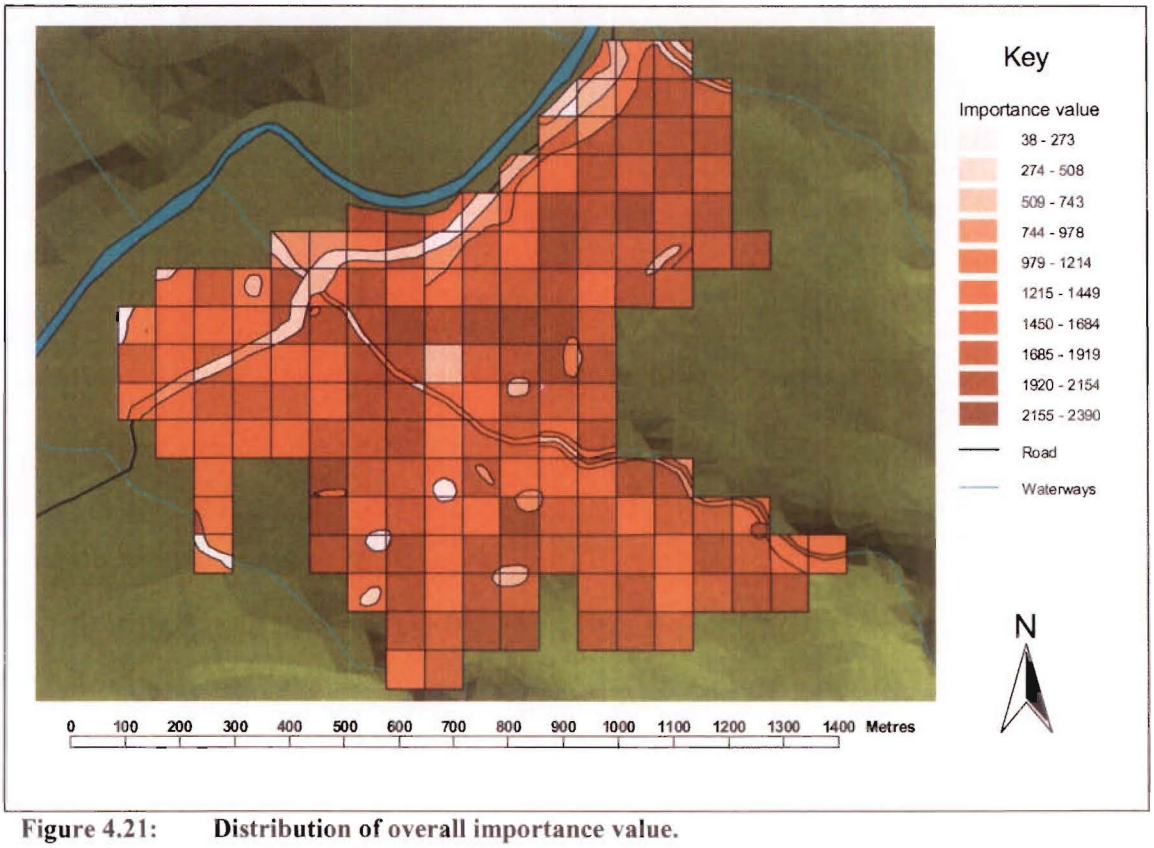

Figure 4.21: Distribution of overall importance value.

4.3.3 Vegetation classification

A comparison of DCA ordinations of species importance values and natural-log-transformed species importance values for all cells confirms the overriding effect of highly abundant *Nothofagus* species on analysis (Figure 4.22 and Figure 4.23).

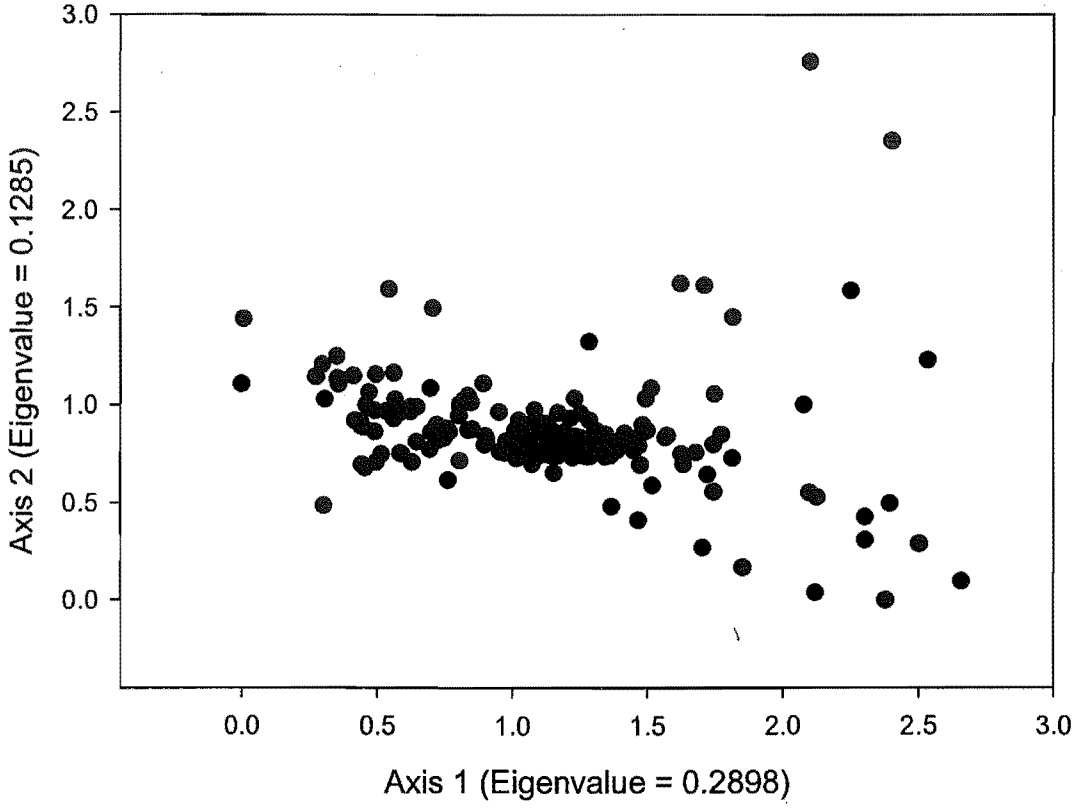

Figure 4.22: DCA ordination of species importance values for all cells.

Much better separation of cells is achieved with the log-transformed data, specifically along the second axis. This change can be primarily attributed to a decrease in the weighting placed on *Nothofagus* species, as *Nothofagus* species were an order of magnitude greater than the next most abundant species within the study site (Table 4.2). This transformation allows more of the heterogeneity attributable to non-*Nothofagus* species to be displayed. Given the strong effect of *Nothofagus* species on analysis and possums' low preference for them, the decision to transform species importance values is vindicated.

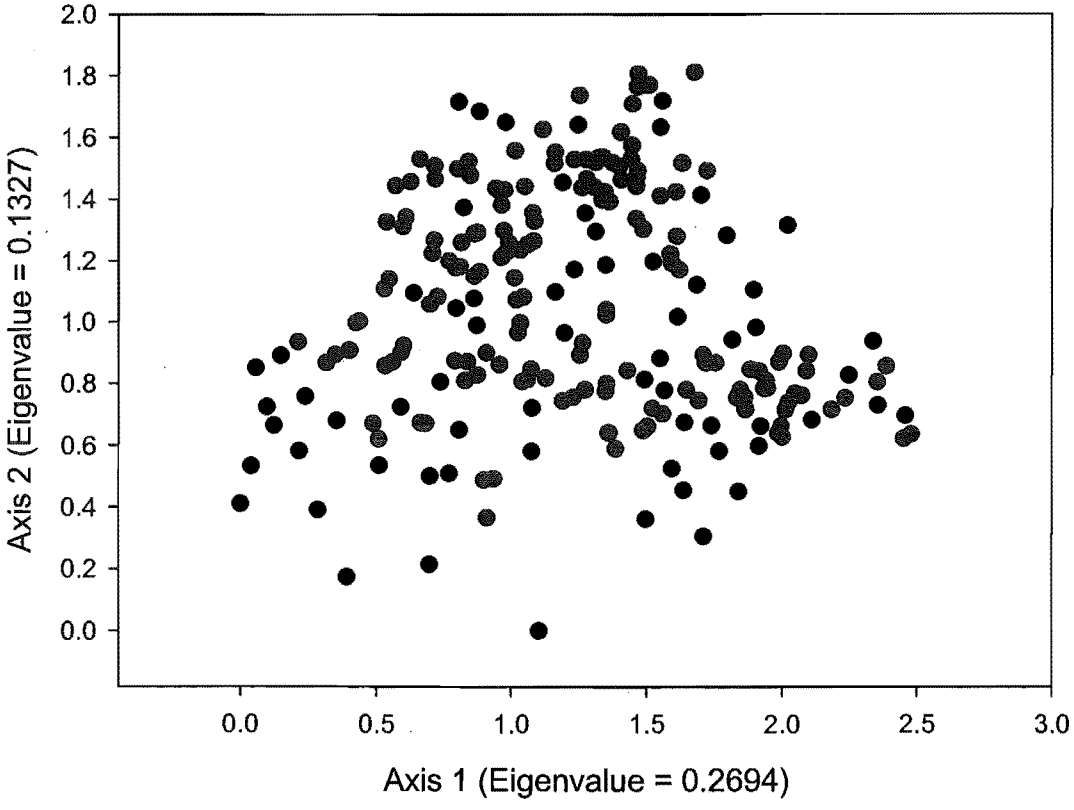

Figure 4.23: DCA ordination of natural-log-transformed species importance values for all cells.

Table 4.1: Pearson correlation coefficients and P-values between ordination axes. U1 and U2 represent the first and second ordination axes for the un-transformed data set, respectively, and T1 and T2 represent the first and second ordination axes for the natural-log-transformed data set, respectively.

Axes	U1	T1	U2	T2
U1	1	-0.79938 <.0001	-0.05881 0.3295	0.17289 0.0039
T1		1	0.03680 0.5419	-0.05634 0.3502
U2			1	-0.40173 <.0001
T2				1

Regardless, the fundamental properties of the ordination axes are retained following the natural-log transformation, as is demonstrated by the high correlations between the ordination axes derived from both the raw and transformed data (Table 4.1).

TWINSPAN classification of the natural-log-transformed importance data yielded three vegetation types (Figure 4.24). The first division in the classification represents a distinction between open and forest sites. All of the indicator pseudospecies for this division are those found along the roadside and swamp areas and are obviously preferential to this group. The eigenvalue for this division is reasonably low; only 27 % of the variation in the data set was used to discriminate the dichotomy. Further divisions of group one were ignored as its constituents formed an intuitively logical unit and subsequent division yielded spurious groups.

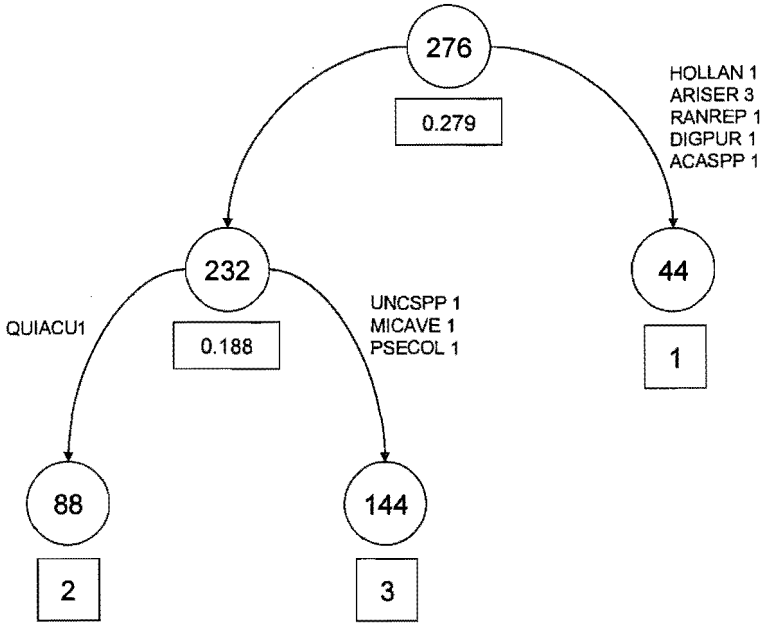

Figure 4.24: Dendrogram of TWINSPAN classification. Circles represent the number of assessment units, rectangles represent the eigenvalue of each separation, squares designate the group number and indicator pseudospecies are displayed for each dichotomy where present (pseudospecies names are a concatenation the first three letters of the genus name and the first three letters of the species name, where known, or 'spp' if not. The number following the pseudospecies name indicates the pseudospecies level, with a larger number representing a higher abundance).

The second division effectively differentiated between areas containing abundant *W. racemosa* and *Quintinnia acutifolia*, and more general terrace areas. Pseudospecies indicators for group three were the monocotyledons, *Uncinia* spp. and *Microlaena avenacea*, and the small tree, *P. colorata*. Although *Q. acutifolia* in low abundance was the only indicator for group two, *Q. acutifolia* and *W. racemosa* were preferential towards this group in all abundances.

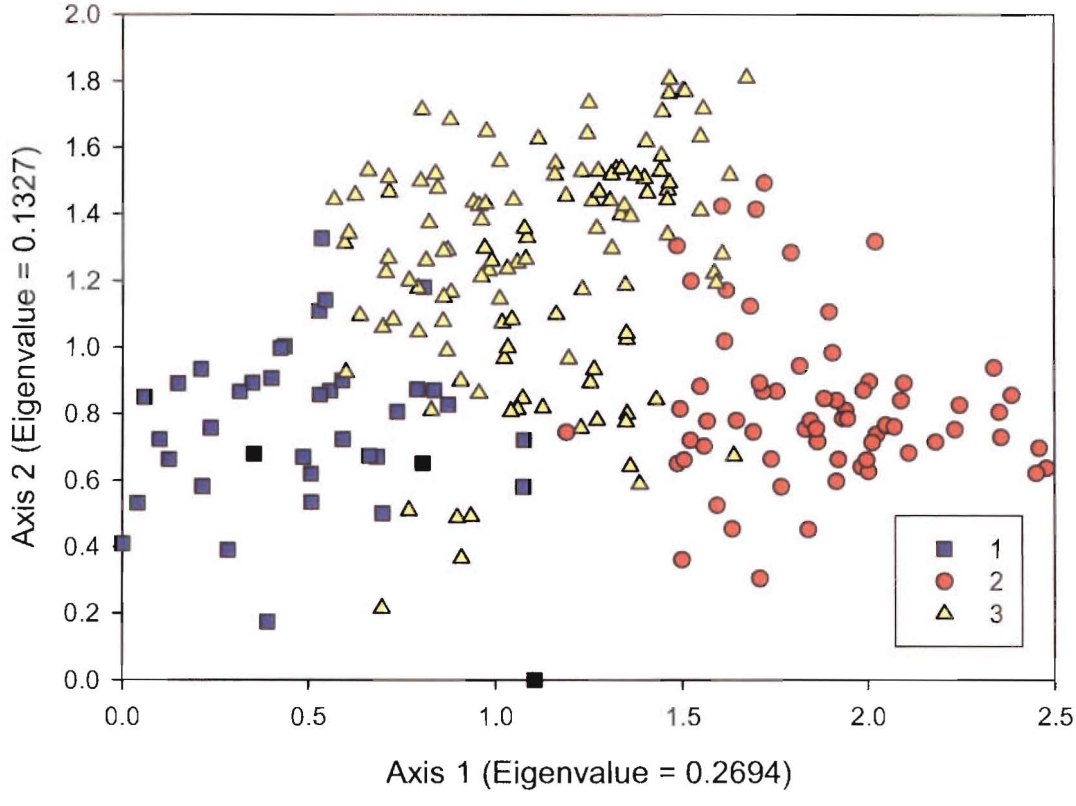

Figure 4.25: DCA ordination of all assessed units plotted on ordination axes one and two (natural-log-transformed species importance values). The key represents vegetation types derived using TWINSPAN.

Results of DCA ordination plotted on the first and second axes indicated considerable floristic overlap between the three vegetation types and little evidence for the presence of floristic discontinuities (Figure 4.25); the variation explained by axis one separates vegetation types one and two well, yet vegetation type three overlaps with each. Floristic separation along axis two is less than that for axis one, but it does

differentiate between vegetation type three and the others, albeit to the same degree as axis one. A plot of the same ordination using the first and third axes indicates that the floristic separation along the third axis is very poor (Figure 4.26).

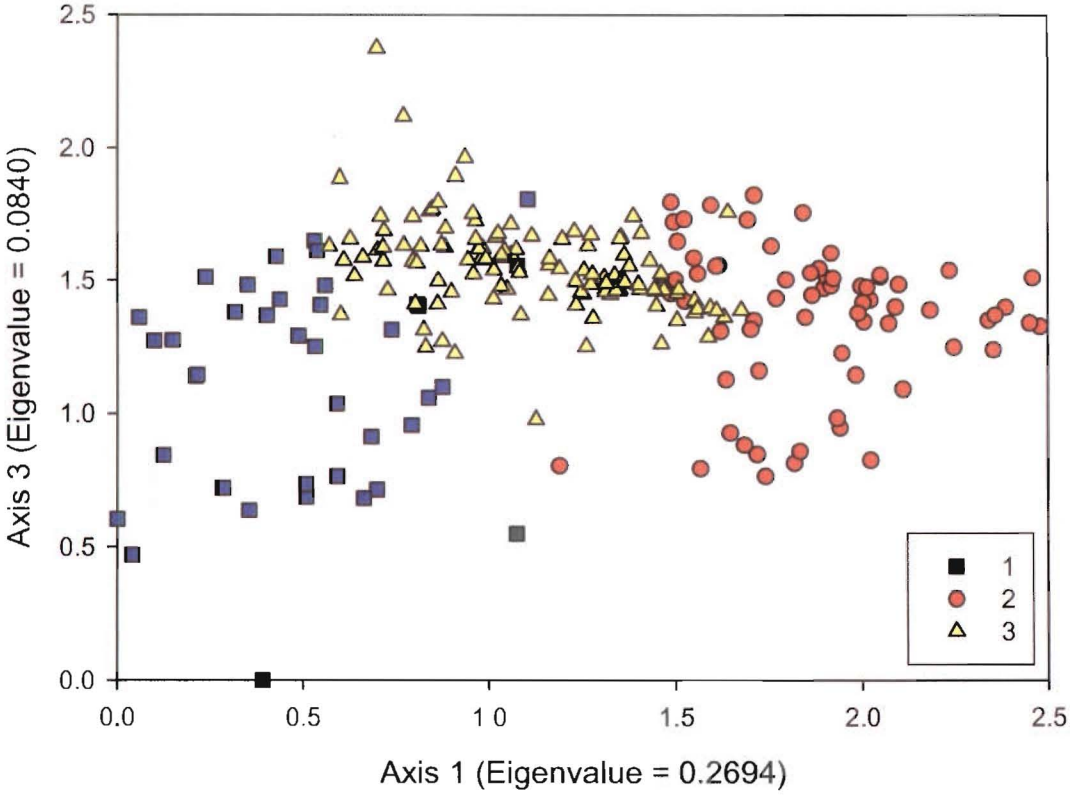

Figure 4.26: DCA ordination of all assessed units plotted on ordination axes one and three (natural-log-transformed species importance values). The key represents vegetation types derived using TWINSPAN.

When individual species are plotted on the primary ordination axes (Figure 4.27) those on the periphery of the cluster represent species that occur in environmental extremes (ter Braak and Prentice, 1988). Roadside species are shown at the left of the plot, species occurring on steep areas are loosely shown at the right and the more generally distributed species such as *N. fusca* and *N. menziesii* are located within the centre of the plot. Strong evidence for distinct species assemblages within the wider data set is lacking, except for the roadside species, which form a reasonably coherent group.

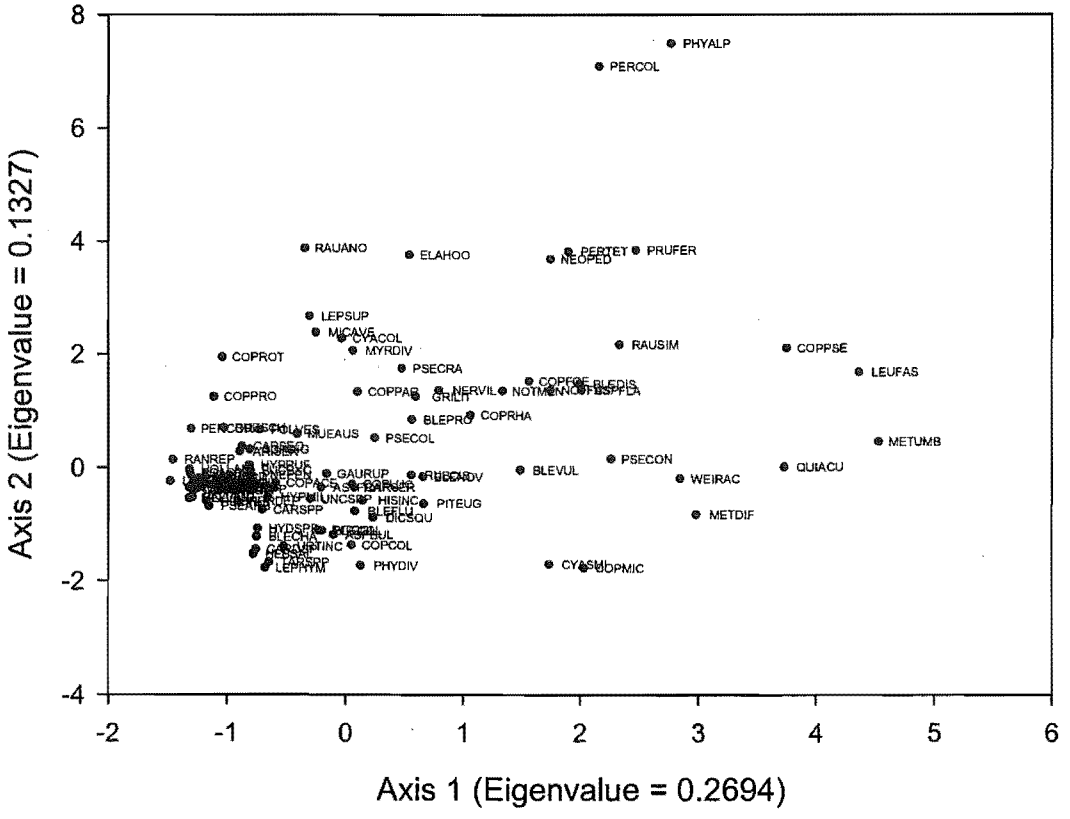

Figure 4.27: Scatter diagram of species following DCA ordination plotted on ordination axes one and two (natural-log-transformed species importance values). Names are a concatenation the first three letters of the genus name and the first three letters of the species name, where known (see Appendix 2 for full names).

4.3.4 Vegetation type descriptions and summaries

The general distribution of vegetation types within the surveyed area can be seen in Figure 4.28 and a more detailed view of the core surveyed region can be seen in Figure 4.29. Common species abundances overall and within vegetation types is summarised in Table 4.2. Species' names are given as a concatenation the first three letters of the genus name and the first three letters of the species name, where known, in order to simplify vegetation type names.

Vegetation type one: Notfus – Notmen // Ariser – (Carser) – (Fucexc) – (Grilit) – (Psecra) – (Coppar) / (Blenov) - (Hollan) - (Hisinc) – (Uncspp) - (Ranrep) – (Bledis) treeland occurred alongside Palmer Road, typically 10-20 m either side of the road

surface. The swamp area below the south west regions of the road was also classified in this vegetation type. Although this type was only a small component of the wider study site (including the surveyed area and the subsequently classified peripheral areas), comprising three percent, it was more extensive in the surveyed region of the study site, comprising five percent of the total surface area.

Figure 4.28: 3D representation of vegetation types within the general study area (type 1 = red/brown, type 2 = yellow, type 3 = olive). Angular borders represent cell boundaries.

The dominance of *Nothofagus* species in this vegetation type is misleading because the coverage of these species was primarily attributable to overhanging branches. More characteristically this vegetation type comprised a dense sward of herbs, introduced grasses and native sedges bordered by clumps of ferns, shrubs and lianes, grading back into mature forest. Although categorised in this vegetation type, the swamp area is worthy of separate mention because of its unique features; this area was dominated by *Carex secta* and included the typically high-altitude species *Astelia nervosa* and *N. solandri* var *cliffortioides*. Nevertheless, the swamp shared many species with the roadside and given the common attribute of negligible canopy cover, the amalgamation of these areas is warranted.

Vegetation type two: Notfus – Notmen / Weirac – Quiacu / (Grilit) – (Coprha) / (Bledis) forest was found on the steeper areas of the study site including the lower hill slope, incised stream and roadside escarpment areas, and comprised 56 % of the wider study area and 39 % of the surveyed region by surface area. *N. fusca* was the clearly the most dominant species followed by *W. racemosa*. *N. menziesii* was only half as abundant as *W. racemosa* in this vegetation type, yet it was a much more important component of the canopy.

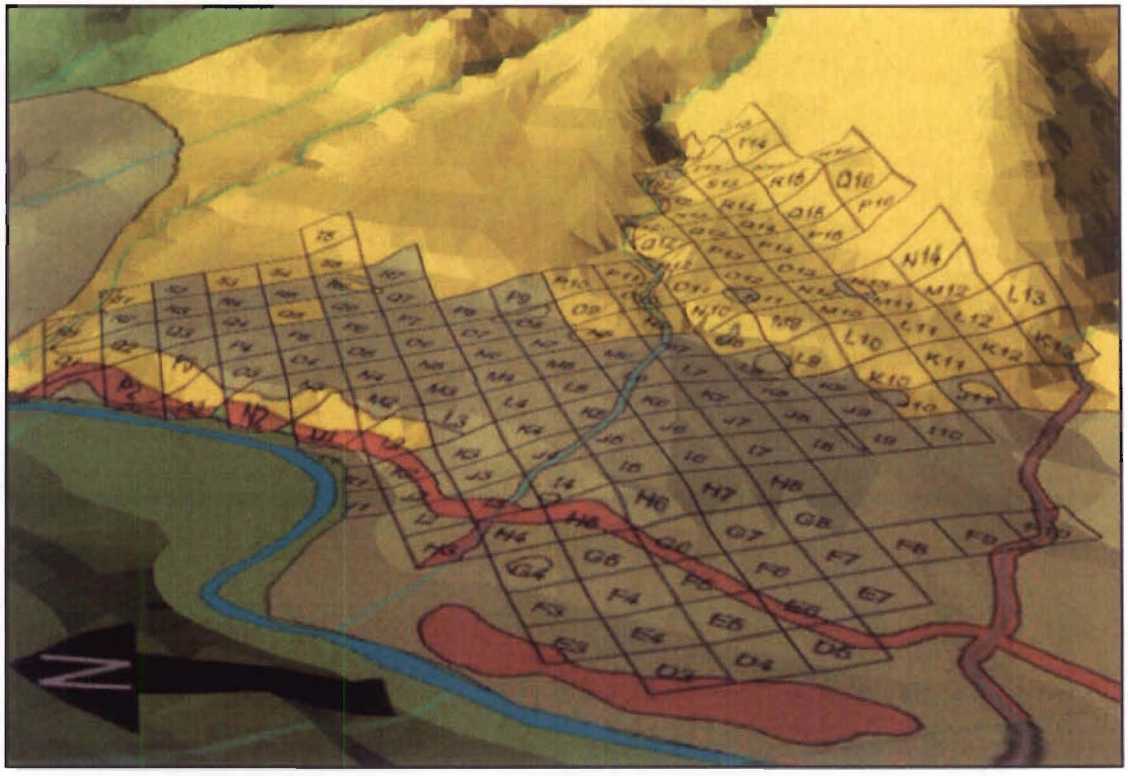

Figure 4.29: 3D representation of vegetation types focusing on the core surveyed area (type 1 = red/brown, type 2 = yellow, type 3 = olive).

This vegetation type was the only one in which *Q. acutifolia* reached high abundance. The dominance of the upper tiers appeared to have suppressed the shrub and ground layers to the point where *B. discolor* and *P. colorata* were the only commonly-occurring lower-tier species. It is likely that the presence of these species is attributable to the transitional area between the hillside and the terrace because they become much less common with increasing slope. This applies especially to *P. colorata*. In steeply sloped areas of the true hillside, *W. racemosa* and *Q. acutifolia*

were very abundant in the subcanopy and shrub tiers, almost to the exclusion of other species except *B. discolor*.

Vegetation type three: Notfus – Notmen // (Psecol) - (Grilit) – (Neoped) – (Carser) – (Psecras) – (Coprha) – (Coppar) / (Bledis) – (Micave) forest occurred on gently sloped interior terrace areas, was the second largest component of the wider study area, comprising 41 %, and was the largest component of the surveyed region, comprising 57 %. This vegetation type occasionally occurred as canopy gaps within vegetation type two. Similar to type two, this vegetation type was dominated by *Nothofagus* species. However vegetation type three differed in that *N. menziesii* was much more abundant, yet the subcanopy tier was less dense (Table 4.2). The decreased density of the subcanopy tier appears to have promoted a greater abundance of lower tier species such as *G. littoralis, Carpodetus serratus, Coprosma parviflora, Neomyrtus pedunculata, Uncinia* spp. and *Microlaena avenacea*. Considerable variation existed in this vegetation type with landform varying from stable, marginally sloped terrace to undulating debris fields with frequent seepages. Consequently, considerable variation in species distributions was also present (e.g. Figure 4.3, Figure 4.7 and Figure 4.5).

Classification lead to significant differences between vegetation type attributes (Table 4.3). As such, some further generalisations can be made:

Vegetation type one is clearly the most diverse and has a significantly greater shrub density than type two. Overall, this vegetation type is the most structurally distinct. Vegetation type two has the greatest slope and subcanopy density, but the lowest species richness. Interestingly though, this type has a significantly greater Shannon diversity index than type three, which suggests that it has greater evenness. Vegetation type three is the most gently sloped of all the types. The structural difference between types two and three is limited to the subcanopy and the ground tiers; type two has a greater subcanopy density yet a lesser ground layer density.

Table 4.2: Species importance values of vascular plant species with > 60 % frequency in any given type. '+' signifies > 60 % frequency with < 1 species importance value in specific type, '-' signifies < 60 % frequency in specific type and blank space indicates not present in specific type. Summaries are also given for structural variables, diversity indices, slope and surface area.

Species	Vegetation type			Overall
	1	2	3	
Nothofagus fusca	263.7 ± 45.8	991.8 ± 43.4	1120.3 ± 39.9	936.0 ± 31.1
Nothofagus menziesii	125.8 ± 26.1	121.1 ± 12.5	369.1 ± 18.7	256.1 ± 13.0
Pseudowintera colorata	-	-	37.8 ± 4.5	23.5 ± 2.6
Blechnum discolor	1.3 ± 0.3	17.3 ± 1.5	20.1 ± 1.1	16.1 ± 0.8
Grisilinia littoralis	6.3 ± 1.3	3.3 ± 0.6	13.1 ± 1.2	9.1 ± 0.7
Pseudopanax crassifolius	3.8 ± 1.0	-	5.6 ± 0.5	4.1 ± 0.3
Coprosma parviflora	3.8 ± 0.9	-	2.6 ± 0.2	2.3 ± 0.2
Coprosma rhamnoides	-	1.5 ± 0.1	2.8 ± 0.2	2.2 ± 0.2
Microlaena avenacea	-	-	1.4 ± 0.3	+
Nertera villosa	-	-	+	+
Weinmannia racemosa	-	299.2 ± 18.9	-	-
Quintinia acutifolius	-	90.9 ± 12.5	-	-
Aristotelia serrata	58.5 ± 8.7	-	-	-
Carpodetus serratus	12.2 ± 1.5	-	7.7 ± 1.8	-
Neomyrtus pedunculata	-	-	10.6 ± 1.4	-
Holcus lanatus	2.9 ± 0.5			-
Histiopteris incisa	2.5 ± 1.0	-	-	-
Blechnum novae-zealandiae	3.6 ± 0.8	-	-	-
Fuchsia excorticata	7.0 ± 2.6	-	-	-
Ranunculus repens	1.8 ± 0.4			-
Muehlenbeckia australis	2.6 ± 0.5	-	-	-
Uncinia spp.	2.0 ± 0.7	-	+	-
Blechnum fluviatile	+	-	-	-
Digitalis purpurea	+			-
Trifolium repens	+			-
Canopy†	170.4 ± 35.7	851.1 ± 41.5	997.1 ± 29.6	813.9 ± 28.2
Subcanopy†	189.4 ± 21.8	546.0 ± 20.6	441.5 ±13.9	425.0 ± 13.0
Shrub†	226.2 ± 21.1	192.6 ± 9.1	212.7 ± 7.2	207.4 ± 6.0
Ground†	22.6 ± 2.1	19.3 ± 0.9	21.3 ± 0.7	20.7 ± 0.6
All tiers	608.6 ± 57.9	1609.0 ± 51.7	1672.5 ± 39.3	1466.9 ± 38.0
Canopy cover (%)	8.6 ± 1.1	51.4 ± 2.2	57.3 ± 2.1	48.6 ± 1.7
Species richness	27.7 ± 1.0	15.8 ± 0.6	19.5 ± 0.4	19.1 ± 0.4
Shannon diversity index	1.55 ± 0.07	1.05 ± 0.02	0.96 ± 0.03	1.09 ± 0.02
Slope (deg)	13.8 ± 1.8	18.8 ± 0.9	10.1 ± 0.4	13.7 ± 0.3
Percentage of total area$^{\psi}$	4.7	38.8	56.5	100.0

† cover abundance multiplied by tier span
ψ the surveyed region

Table 4.3: Mean differences between vegetation types following pairwise comparisons with Tukey's studentised range test. Differences represent the product between the values of the positive and negative vegetation types. The terms 'positive type' and 'negative type' are simply used to indicate the direction of differences in pairwise comparisons of vegetation types. '+' indicates significantly greater, '-' indicates significantly lesser and 'ns' indicates no significant difference ($p<0.05$).

Variable	Negative type	Positive type		
		1	2	3
Canopy importance value	1		+	+
	2	-		ns
	3	-	ns	
Subcanopy importance value	1		+	+
	2	-		-
	3	-	+	
Shrub importance value	1		-	ns
	2	+		ns
	3	ns	ns	
Ground importance value	1		ns	ns
	2	ns		+
	3	ns	-	
All tiers importance value	1		+	+
	2	-		ns
	3	-	ns	
Canopy cover	1		+	+
	2	-		ns
	3	-	ns	
Species richness	1		-	-
	2	+		+
	3	+	-	
Shannon diversity Index	1		-	-
	2	+		-
	3	+	+	
Slope	1		+	-
	2	-		-
	3	+	+	

As is to be expected, many of the tier importance values are highly correlated (Table 4.4). The most highly correlated are the canopy and subcanopy tiers (one and two, respectively). This positive relationship is driven by canopy trees that also have significant foliage in the subcanopy tier. High canopy abundance appears to suppress the shrub tier to the benefit of the ground tier, while the subcanopy tier does not appear to have any significant influence on these lower tiers.

Table 4.4: Pearson correlation coefficients and P values for forest tier structure (N = 275).

Stratum	Tier1	Tier2	Tier3	Tier4
Tier1	1	0.543 <.0001	-0.107 0.0777	0.192 0.0014
Tier2		1	0.025 0.6818	-0.064 0.2870
Tier3			1	-0.134 0.0269
Tier4				1

4.3.5 Phenology

New growth for all species was found to increase dramatically in spring and to plateau in summer. No new growth was observed in late autumn/winter. While new growth was impractical to assess for *T. repens*, previous work in New Zealand has indicated that new growth is most common from spring through to summer, with the lowest abundance of foliage occurring in winter (Brougham, 1962). Foliage loss exceeds foliage gain during autumn and winter months (Kemp *et al.*, 1999), which leads to the decrease in leaf area index (LAI) observed in Figure 4.30. *M. australis* new growth first appeared in early spring, and reached highest abundance in late spring. New growth continued to be produced throughout summer. Flowers occurred in late spring and continued at lower abundance through to mid-summer (Figure 4.31). Fruit was most abundant in early autumn.

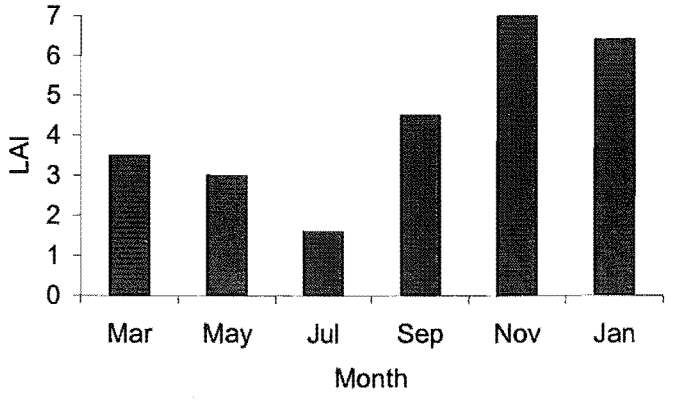

Figure 4.30: Change in leaf area index (LAI) of *Trifolium repens* by month, reproduced from Brougham (1962). LAI represents the surface area of all leaves on a plant.

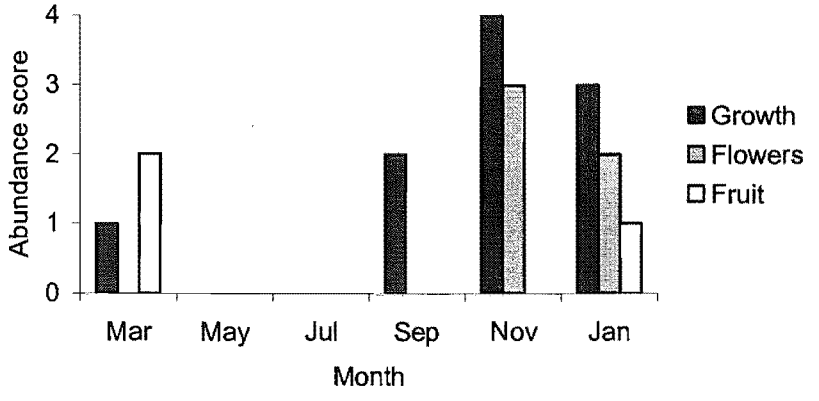

Figure 4.31: Change in abundance of *Muehlenbeckia australis* new growth, flowers and fruit by month.

A. serrata new growth was most abundant in the spring and summer months, yet flowers were only present during late spring (Figure 4.32). *A. serrata* fruit was similarly short-lived in abundance, only occurring in mid-summer.

F. excorticata flowers and fruit were more evenly distributed between the months than *A. serrata*, with flowers appearing in early spring and continuing through to mid-summer, and fruit appearing in late spring and continuing through to their highest abundance in mid-summer (Figure 4.33). The flush of new growth on *F. excorticata* was similar to that of *A. serrata*, reaching peak abundance in late spring and continuing through to mid-summer.

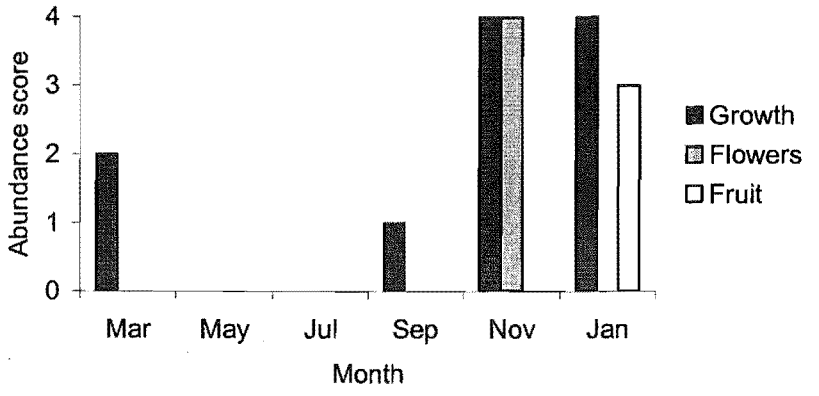

Figure 4.32: Change in abundance of *Aristotelia serrata* new growth, flowers and fruit by month.

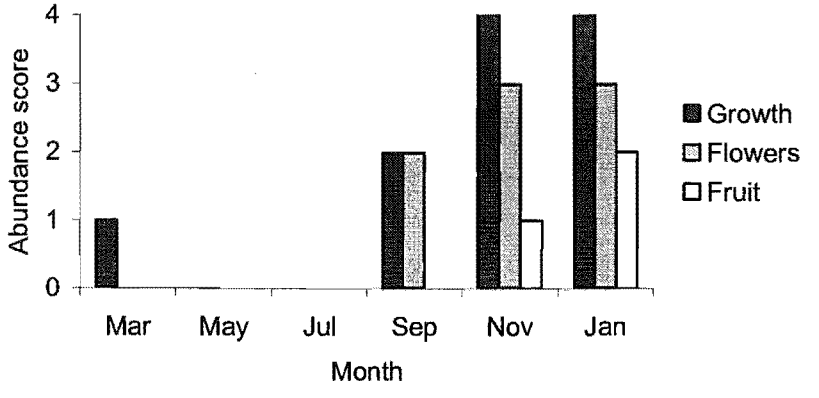

Figure 4.33: Change in abundance of *Fuchsia excorticata* new growth, flowers and fruit by month.

Similar to *A. serrata* and *F. excorticata*, *W. racemosa* new growth was most abundant in late spring, remained abundant throughout summer and tapered off in early autumn (Figure 4.34). *W. racemosa* flowers were relatively late to appear, only occurring in mid-summer when they were highly abundant. Fruit production was not quantified for this species.

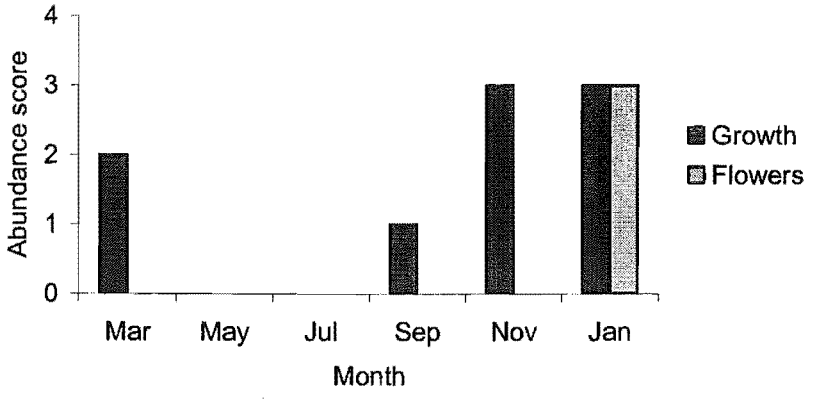

Figure 4.34: Change in abundance of *Weinmannia racemosa* new growth and flowers by month.

Epigeous fungal sporocarps reached maximum abundance in autumn and persisted in moderate abundance throughout winter (Figure 4.35). A slight increase in abundance was observed in late spring and was followed by a decrease in abundance during summer.

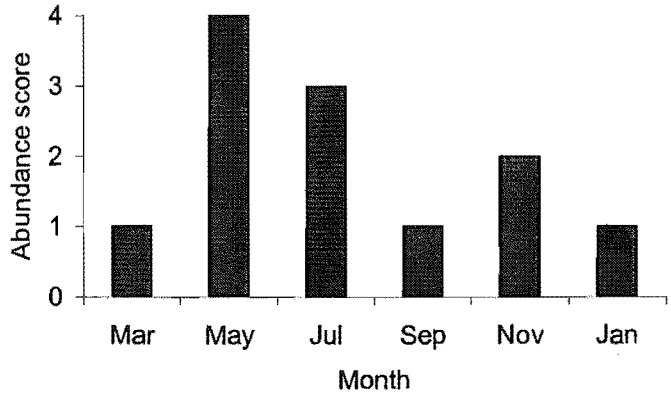

Figure 4.35: Change in epigeous fungal sporocarp abundance by month.

The spatial distribution of sporocarps appeared to be associated with decaying organic matter such as coarse woody debris and leaf litter. The greatest abundance of this decaying material occurred within the true forest areas, which excludes the roadside and swamp areas. Consequently, the greatest abundance of sporocarps occurred within terrace and hillside areas.

4.4 Discussion

4.4.1 Contextual vegetation comparison

On a regional scale, the study forest represents a transition from dry eastern mountain beech forest to wetter western mixed beech/podocarp/broad-leaved forest (Wardle, 1974; Wardle, 1984). However, in more specific terms the forest at the study site appears to be comprised of a mixture of Wardle's (1974) low-level *N. menziesii / N. fusca* (D2) and *N. fusca / W. racemosa / Q. acutifolia* (E1) classifications. When compared to the vegetation types derived in this study, Wardle's (1974) D2 approximates vegetation type three and E1 approximates vegetation type two. A detailed study conducted at nearby (c. 15 km to the NW) Mt Harata using TWINSPAN and ordination analysis (Stewart *et al.*, 1993) also identified vegetation communities similar to those in this study. These were *N. fusca – W. racemosa* forest (community B4), similar to vegetation type two, and *N. fusca – N. menziesii* forest (community B1), similar to vegetation type three. Community B4 was found to be associated with more recent soils than community B1 (Stewart *et al.*, 1993) and this relationship is likely to hold true at the Palmer Road site, as *N. menziesii* was more abundant and *W. racemosa* less abundant on stable landforms. Despite these similarities, the Mt Harata study site possessed more abundant broad-leaved and podocarp species than the Palmer Road study site, which reflects its closer proximity to the coast and higher rainfall. Such an observation highlights the transitional nature of this area with respect to vegetation composition.

Comparisons between the Palmer Road study site and other *Nothofagus* dominated sites where possum research has been conducted are hindered by the paucity of detailed vegetation descriptions at these sites. However, the nearest sites are likely to be the most similar. Accordingly, the most similar study forest to the Palmer Road study forest occurred at the nearby (c. 18 km to the NE) Arnold River (Pekelharing *et al.*, 1998a). This *N. fusca / N. menziesii* dominated terrace forest shared many palatable plant species with the Palmer Road study site, with the notable exception of *W. racemosa.* The next most similar site occurred in the north branch of the Hurunui Catchment (c. 30 km to the south) and was used for a possum diet study (Sweetapple, 2000). This mixed *N. fusca / N. menziesii* forest appeared to be simpler in terms of

species richness than the forest found at Palmer Road, probably due to a lower rainfall and higher altitude. As such, many of the typical possum palatable species found at Palmer Road were rare or absent.

Another possum study was conducted in the Nelson Lakes National Park on the slopes of Mt Misery (c. 75 km to the NE) and associated alluvial flats (Clout and Gaze, 1984). The lower areas of this study site were dominated by *N. fusca* and *N. menziesii*, but, in contrast to the Palmer Road forest, also included an emergent podocarp component. *P. colorata*, *Coprosma rotundifolia* and *F. excorticata* were common in the lower tiers, and, similar to the Palmer Road study forest, *W. racemosa* occurred in highest abundance on the lower slopes of the mountain.

The remaining *Nothofagus* forests where possum research has been conducted can be tentatively placed into a *N. menziesii* dominated group. These studies included landform types such as river valleys, mountains, moraines and hill country (Rose *et al.*, 1993; Owen and Norton, 1995; Pekelharing *et al.*, 1998b; Cochrane and Norton, 2000). Despite the difference in canopy dominants, these sites contained many of the palatable species found at the Palmer Road study site, such as *F. excorticata*, *A. serrata*, *M. australis*, *W. racemosa* and *Pseudopanax* spp. (Rose *et al.*, 1993; Owen and Norton, 1995; Pekelharing *et al.*, 1998b; Cochrane and Norton, 2000).

When placed in context with the other *Nothofagus* forests, it appears that the Palmer Road study forest represents wet *N. fusca* / *N. menziesii* forest. Although generally similar to many of the other *N. fusca* / *N. menziesii* forests studied elsewhere, the forest studied here contains a greater diversity and abundance of palatable species.

4.4.2 Forest heterogeneity

4.4.2.1 Structure

Throughout the forest an increasing canopy density was related to a decreasing shrub density and an increasing ground density. These relationships are likely a result of the competitive influence of hierarchical light interception; dense canopies inhibit the growth of shrubs to the benefit of ground tier plants, such as *B. discolor*. Because this

effect is hierarchical, the most influential factor on forest structure is canopy density, which in turn is dictated by frequency of disturbance. Because disturbance is stochastic, the pattern of forest structure is also largely stochastic. However, landform does exert some influence over disturbance through the process of mass movement and the effect of topography on wind currents; steep areas are likely to experience frequent mass movement and lower lee slopes are highly susceptible to wind damage (Wardle, 1991).

Mature *Nothofagus* trees, in particular *N. fusca*, clearly dominated vegetation types two and three. Combined, these types represented 95 % of the study site by surface area, yet when one considers that possums occupy a three dimensional habitat in forested areas (Ward, 1978) their effective contribution to potential possum habitat is likely to have been even greater because they are the sole representatives of tall forest. When types two and three are compared, the structural importance values only differ between the subcanopy and ground layers. There is no significant correlation between these attributes and, therefore, they should be viewed as indicators of separate processes.

The structure of vegetation type one is markedly different from that of types two and three. Most obvious is the lower density of the upper tiers in type one. Despite this lack of upper tier density, shrub density in type one is only greater than that in type two, a likely reflection of the inhibitory effect of grass swards and stock grazing pressure on shrub regeneration in type one.

4.4.2.2 Composition

Although structural variation within the majority of the study forest was low, the same can not be said of species composition. When species associations are considered, there is a high degree of separation between open (vegetation type one) and closed forest (vegetation types two and three). DCA ordination indicated that species found in open sites infrequently occurred with most of the typical forest species. Additionally, species distributions indicated that there were significant and abrupt changes in abundance across boundaries between open and closed areas.

Such boundaries did not exist between the closed forest vegetation types; change in species abundance was much less consistent and pronounced. In these areas species' abundance distributions did show pattern, but the form of these patterns differed markedly between species and were frequently nested in stochastic variability. It appears as though the distributions of most species within the forested areas are highly dependent on disturbance. Evidence for this can be found in the influence of disturbance on *Nothofagus* spp. abundance and the exclusive effect of *Nothofagus* spp. abundance on other species abundance.

The greatest distinction between type two and three was the abundances of *W. racemosa* and *Q. acutifolia*, as indicated by their preferentiality towards vegetation type two following classification with TWINSPAN. However, this distinction was only evident at a coarse spatial scale. Fine-scale examination indicated that their abundance distributions best approximated gradients and that the imposition of a boundary between types two and three divides these gradients in an arbitrary way. This is a major limitation of TWINSPAN classification; TWINSPAN relies on continuum segmentation instead of identifying true clusters in data (Carleton *et al.*, 1996). Although TWINSPAN does have the potential to recognise discontinuities within vegetation data, the presence of discontinuities is not explicitly recognised and, consequently, TWINSPAN classification often yields indistinct vegetation types (van Groenewoud, 1992).

Vegetation type one is clearly the most floristically diverse; elsewhere the dominance of *Nothofagus* species suppresses diversity of lower tiers, whereas open areas promote the formation of swards containing numerous species of monocotyledons and herbs. This high light environment also promotes high abundance of many species that exist within the forested areas in low abundances, such as *A. serrata* and *F. excorticata*.

When the distribution of palatable species is considered, the differences between vegetation types become highlighted. The bulk of these species were most abundant in vegetation type one, with the northern roadside areas, in particular, containing the highest abundance of *A. serrata*, *F. excorticata* and *M. australis*. In the true forested areas, vegetation types two and three, the most abundant palatable species was *W. racemosa*, with the highest abundance of this species occurring on the steepest

areas. Other palatable species did occur in these areas, but at low abundance and most commonly associated with canopy gaps.

It appears that the vegetation types classified at the Palmer Road study site make a useful distinction between open and closed forest areas and between steeply and gently sloping areas of the forest. These vegetation types embody a large component of palatable species heterogeneity, yet it must be recognised that the boundary between types two and three is artificial because it does not follow any natural discontinuity in species' gradients.

4.4.2.3 Phenology

Seasonality in possum diet reflects the availability pattern of seasonally abundant food sources such as new growth, flowers and fruit (Cowan, 1990b; Nugent *et al.*, 1997). Although many of these food sources are ephemeral, they can contribute a great deal to possum diet when and where they are abundant. Indeed, *W. racemosa* flowers were found to be the most important food item in one sample of possum stomachs collected in the Palmer Road study site (Cochrane *et al.*, 2003). The timing of availability of these seasonal food sources, combined with their spatial heterogeneity is likely to have effects on possum feeding behaviour. Specifically, this effect is likely to be manifested as diet switching in relation to food source availability (Owen and Norton, 1995).

Phenological observations made at the Palmer Road study site indicate that the highest availability of seasonal food resources occurred from early spring through to late summer. The phenological patterns of new growth, flower and fruit production observed at the Palmer Road study site appear congruent with observations made at other areas of New Zealand. Observations on *A. serrata*, *F. excorticata* and *W. racemosa* in the central North Island at sites similar in altitude to the Palmer Road study site indicate that initiation and duration of new growth production is reasonably consistent between these North Island sites and the Palmer Road study site (Leathwick, 1984). Phenological observations made in Dunedin indicated that new growth was initiated in early August for both *A. serrata* and *F. excorticata*, and continued until March (Bussell, 1968). New growth initiation in *W. racemosa* has

been observed to occur in Westland at a similar time to new growth initiation at the Palmer Road study site as well (Wardle, 1966).

Slight temporal variability regarding new growth initiation between sites is likely correlated with temperature. Evidence of this can be found in *F. excorticata*, which exhibits a strong tendency to initiate new growth later with increasing latitude and altitude (Godley and Berry, 1995). Maximum abundance of new growth in most palatable species at the Palmer Road study site was observed to occur between late spring and mid summer, as has been observed in other sites in New Zealand (Bussell, 1968; Leathwick, 1984).

In contrast to the consistency of new growth initiation and length of duration, the initiation, duration and extent of flower and fruit production, appears to vary markedly between sites. Initiation of *W. racemosa* flower production has been observed to occur as early as September, but most commonly occurs in November (Wardle, 1966; Leathwick, 1984; Perott and Armstrong, 2000). The initiation of *W. racemosa* flower production at Palmer Road was later than this, occurring in December. *A. serrata* fruiting at nearby Arnold River has been observed to occur at times similar to those observed at the Palmer Road study site (Pekelharing *et al.*, 1998a). However, observations in the central North Island indicated earlier production and longer duration of *A. serrata* fruit (Leathwick, 1984; Perott and Armstrong, 2000). Differences in the season of maximum abundance of flowers and fruit within the Palmer Road study site were evident between species. *W. racemosa* flowers were very ephemeral, only occurring in high abundance in summer. Similarly, *A. serrata* flowers were most abundant in late spring and maximum fruit abundance followed in mid summer. Maximum *F. excorticata* flower abundance occurred between late spring and summer, and was followed by maximum fruit abundance in summer.

The temporal abundance pattern of epigeous fungal sporocarps contrasted with that of new growth, flowers and fruit, reaching maximum abundance in early autumn. The pattern of epigeous fungal sporocarp abundance observed at the Palmer Road study site is typical of the pattern displayed in other forests (North *et al.*, 1997) and is likely linked to the interaction between soil temperature and moisture (Stevenson, 1994).

Warm temperatures and high soil moisture content in autumn result in a surge of sporocarp abundance and similar conditions in spring produce another, smaller surge (Stevenson, 1994).

Given that the abundance of other important seasonal food sources, such as new growth, fruits and flowers, declines in the autumn months, the high abundance of sporocarps at this time affords possums the opportunity to compensate their diet. Indeed, there are indications that epigeous sporocarps are consumed more frequently between late summer and autumn in the study site (Cochrane *et al.*, 2003). Despite not being assessed in the vegetation survey, observations indicated that sporocarps were patchily distributed throughout the study site, although low heterogeneity has been observed in other forests (North *et al.*, 1997).

4.4.3 Classification approach

Suppressing dominant species in classification analysis is not an uncommon approach, but more commonly rare species are the ones excluded or down-weighted to avoid bias they may impose on classification or ordination (Hill, 1979; Kent and Coker, 1992; ter Braak and Smilauer, 1998). Nevertheless, it must be recognised that most vegetation classification proceeds at large scales (> 1000 ha), where vegetation heterogeneity is high and species dominance is variable (e.g. Atkinson, 1985; Norton and Leathwick, 1990; La Roi, 1992; Burns and Leathwick, 1996; Hahs *et al.*, 1999). The fine scale of this study site and the low level of heterogeneity in both species dominance and environmental factors rendered classification difficult with common approaches.

The dominance of *Nothofagus* species combined with their continuous distribution in the Palmer Road study forest would likely have occluded observation of the heterogeneity of other species. This effect can be conceptualised as 'noise' attributable to stochastic variability within a species, as opposed to variability correlated to environmental factors (Gauch, 1982). The supression of 'noisy' species in analysis is a valid approach and often results in improved clarity of important underlying patterns (Dale *et al.*, 1991). Furthermore, when the unpalatability of *Nothofagus* species is considered, the influence of their heterogeneity on classification

analysis is likely to yield communities with few inferences for possum behaviour. It could be argued that factors other than palatability could have contributed to the *Nothofagus* species' importance. However, unforeseen qualities of these species are unlikely to have elicited a highly variable response by possums because of the low heterogeneity of these species throughout the study site.

4.5 Conclusions

The *N. fusca / N. menziesii* forest at the Palmer Road study site is broadly similar to other *N. fusca / N. menziesii* forests involved in past possum research. However, overall diversity within the study forest was high when compared to other *Nothofagus* forests because it was located in a transitional area between *Nothofagus* forests and mixed *Nothofagus* / broadleaved / podocarp forest (Wardle, 1984).

The most clearly defined heterogeneity within the study site existed between open and closed forest areas. Most palatable species achieved greatest abundance in open areas, yet *W. racemosa* occurred in high abundance within the closed forest areas. Heterogeneity within the closed forest areas was less easily defined. As such, the boundary between vegetation type two and three was somewhat arbitrary, although it did provide a useful distinction between the vegetation found on steep areas and that found on gently sloping areas.

Findings from this chapter represent an approximation of the assemblage of resources available to foraging possums within the study site. As such, species abundances, species distributions and vegetation communities are integrated with possum movement parameters within the following chapter in order to assess resource selection.

Chapter 5: Resource Selection

5.1 Introduction

All organisms are distributed patchily throughout the environment in accordance with their ecological requirements for survival and reproduction (Brown and Orians, 1970; Southwood, 1977; Morrison *et al.*, 1992; Krebs, 1994; Drickamer *et al.*, 1996). This distribution, determined by physiological adaptation, behavioural mechanisms, biotic interactions, abiotic processes and stochastic processes operates at multiple scales (Mackey and Lindenmayer, 2001) and is commonly accepted as the expression of resource selection (Cody, 1985; Rosenzweig, 1985; Wiens, 1989a; Orians and Wittenberger, 1991; Drickamer *et al.*, 1996).

The term 'selection' is, by definition, inexorably linked to the term 'choice'. When animal behaviour is considered, a distinction needs to be made between conscious choice and instinctual choice; conscious choice constitutes only a small component of the overall selection process, as more commonly selection occurs as an automatic reaction to certain key aspects of the environment (Hutto, 1985; Drickamer *et al.*, 1996). Although choices may appear to be discrete or independent, they are invariably influenced by external and historical factors. For example, the choice of where an animal lives is largely determined by where it was born, over which it has no choice. As such, resource selection should be viewed as a hierarchical process (Johnson, 1980; Hutto, 1985; Wiens, 1985; Orians and Wittenberger, 1991) whereby the opportunity of choice is afforded by previous choices made not only by an individual but also by its forebears, conspecifics and heterospecifics.

In a pragmatic attempt to simplify resource selection analyses Johnson (1980) proposed a natural ordering of this hierarchical process which states that:

- first order selection determines the physical or geographic range by a species;
- second order selection determines the location of an individual's home range within the species' physical or geographic range;

- third order selection determines the use of habitat components within the chosen home range;
- fourth order selection determines the consumption of specific resources within habitat components.

This hierarchical approach is unifying in nature as it makes no qualitative distinction between the various orders of selection and it recognises that selection at any level is a product of the selection choices preceding it (Figure 5.1) (Johnson, 1980; Orians and Wittenberger, 1991).

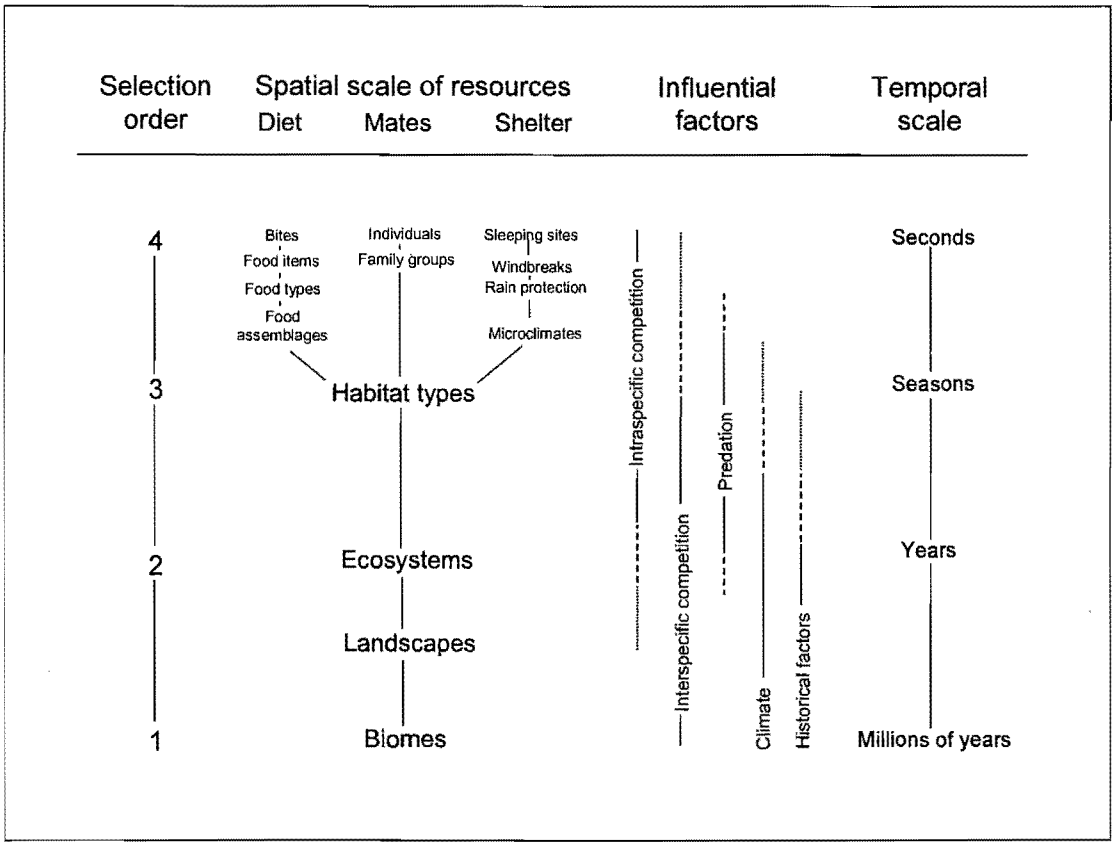

Figure 5.1 Conceptual model of the scales involved in resource selection including influential factors. Nomenclature follows Forman and Godron (1986).

Because of this, inferences provided by resource selection analysis are critically dependent on the scale at which they are studied (Morris, 1987; Orians and Wittenberger, 1991; Poizat and Pont, 1996) and may result in spurious management recommendations if key spatial scales are not considered synchronously (Johnson, 1980; Thomas and Taylor, 1990). Typically, resource selection is assessed at

Johnson's (1980) second and third order scale (Wilson *et al.*, 1998) because these scales are likely to hold the most practical inferences for wildlife managers.

Preference is perhaps the most misused term in the resource selection literature, primarily as a result of the confounding aspect of resource availability. Commonly used as a synonym of selection (Thomas and Taylor, 1990; Marzluff *et al.*, 2001), preference, under its most literal definition, is the likelihood that an individual or population will choose a resource given equal availability of all resources at the chosen scale (Johnson, 1980; Norbury and Sanson, 1992). Used as such, preference can be deemed independent of availability and indicative of the explicit value of a particular resource to a particular individual. Selection, in contrast, is the actual choice made when availabilities are not equal (Johnson, 1980). Therefore, individuals are said to be selective if they utilise resources disproportionate to their availability; the level of this disproportion defines their relative preference for these resources (Johnson, 1980).

Resource selection theory can be considered as a branch of optimal foraging theory (OFT) (MacArthur and Pianka, 1966; Rosenzweig, 1985; Hughes, 1993) because preferential selection of resources implies optimising behaviour (Rosenzweig, 1981). OFT predicts that animals will seek to maximise fitness (Stephens and Krebs, 1986) by utilising a heterogeneous environment in the most efficient and profitable way (MacArthur and Pianka, 1966; Kamil *et al.*, 1987). Central to this theory is the concept of patches or habitats, which are clumps of key resources, or are simply heterogeneous with respect to key resource distribution (MacArthur and Pianka, 1966; Stephens and Krebs, 1986). Under the OFT, animals are expected to show preference for patches that provide the most favourable product of benefits obtained and costs incurred whilst foraging (Charnov, 1976; Rosenzweig, 1981). Although the benefits gained by foraging are dependent on patch quality (Abrams, 1991), the costs incurred while foraging are largely dependent on the spatiotemporal distribution of resources (Laca and Demment, 1991; Turner *et al.*, 1997; Brown, 2000). Consequently, the spatiotemporal variability of key resources must be incorporated into resource selection study designs in order to obtain outcomes that are robust and meaningful.

Numerous resource selection study designs and statistical analyses have been developed, and from these a distinction can be made between those that utilise modelling methods and those that make comparisons between resource use and availability. Statistical modelling approaches are most commonly applied to populations in order to represent abundance as a function of continuously or discretely distributed resource variables (Morrison *et al.*, 1992). Comparisons of resource use and availability are most commonly applied to individuals and require resources to be categorised into discrete entities (Lechowicz, 1982; Loehle and Rittenhouse, 1982; Thomas and Taylor, 1990; Alldredge and Ratti, 1992). The results from such analyses can be scaled up to make population inferences. Comparisons between use and availability of resources are hindered by two key aspects; the first relates to how a resource is defined and the second relates to how availability of resources is defined.

The definition of what constitutes a resource unit is critical and can dramatically affect the outcome of resource selection analyses (Morris, 1987; Rettie and McLoughlin, 1999). Typically, resource units are defined as habitats or patches. These are most commonly perceived as discrete and internally homogeneous (Krebs, 1994), yet such entities are rarely observed in nature (Kotliar and Wiens, 1990). However, the level of heterogeneity and the definition of patch boundaries are dependent on the scale at which they are observed (Forman and Godron, 1986; Wiens, 1989b; Kolasa and Rollo, 1991; Hansen and di Castri, 1992), and are, consequently, biased by the perceptions of the observer (Kotliar and Wiens, 1990). These perceptional biases may lead to a discrepancy between the way an environment is classified by the researcher and the way it is perceived by the study organism, which will yield spurious outcomes. Biases can be mitigated by examining resource selection at multiple scales (Morris, 1987; Kotliar and Wiens, 1990), and by basing classifications on criteria that posses influential consequences for individual fitness (Lidicker, 1999; Rettie and McLoughlin, 1999).

The definition of which resources are available and how available they are is perhaps the most crucial assumption of resource selection studies. However, this definition is frequently an arbitrary one (Johnson, 1980; Porter and Church, 1987; Warnock and Takekawa, 1995; Arthur *et al.*, 1996; McClean *et al.*, 1998). Factors such as the behavioural strategies of the study animal and spatiotemporal change of resource

quality play an important role in determining the actual availability of resources (Porter and Church, 1987; Orians and Wittenberger, 1991; Otis, 1998; Wilson *et al.*, 1998; Rosenberg and McKelvey, 1999). This is the reason why field studies of resource selection can never determine true resource preference; given current techniques, availability of a resource to an individual can not be completely accounted for (Marzluff *et al.*, 2001). Nevertheless, for the purposes of this thesis, the term 'preference' will be used as an approximation of true preference in recognition of the limitations outlined above.

Modelling as a means of habitat selection analysis avoids many of these problems as the environment does not require classification and availability of resources need not be defined. These approaches simply seek to find relationships between the abundance of, or usage by, the study organism and the levels of measured resources or environmental variables. Modelling approaches can be defined as either hindcasting or forecasting depending on the intended use and information available; hindcasting can be viewed as an exploratory tool, whereas forecasting seeks to develop predictive power that can be applied to areas outside of the study site (Morrison *et al.*, 1992).

Possums, as generalist herbivores (Statham, 1984; Cowan, 1990a), are faced with foraging decisions strongly influenced by vegetation quality and abundance (Illius and Gordon, 1993). Under simplistic OFT, possums are expected to select resources that maximise fitness and therefore select areas that contain such resources. Furthermore, because vegetation quality and abundance exhibits temporal variability, possums are expected to exhibit temporally variable selection patterns also (Armstrong *et al.*, 1987). However, it must be recognised that foraging decisions are also influenced by factors not explicitly related to diet, such as competition, social interaction and predation (Sih, 1993). The mechanisms by which these factors influence possum foraging are complex and poorly understood, and are outside of the scope of this study.

An investigation of multi-scale resource selection by possums may elucidate important relationships between levels of utilisation and resource properties. The fundamental question being asked is: how do possums respond to spatiotemporal resource heterogeneity? Possum diet has been studied extensively (Gilmore, 1967;

Fitzgerald, 1978; Warburton, 1978; Fitzgerald and Wardle, 1979; Fitzgerald, 1984; MacLennan, 1984; Statham, 1984; Coleman *et al.*, 1985; Cowan and Moeed, 1987; Cowan, 1990b; Brown *et al.*, 1993; Owen and Norton, 1995; Allen *et al.*, 1997; Nugent *et al.*, 1997; Nugent *et al.*, 2000; Cochrane *et al.*, 2003), yet very little attempt has been made to make diet selection spatiotemporally explicit. Similarly, research on possum movements has infrequently included comprehensive investigation into the underlying drivers of movements (e.g. Crawley, 1973; Ward, 1978; Thomas *et al.*, 1984; Brockie *et al.*, 1989; Brockie *et al.*, 1997; Statham and Statham, 1997). Given the importance of spatiotemporal factors to both possum control and monitoring, investigations into the processes governing space use may be beneficial for improving their efficacy.

The primary objectives of this chapter are to:

- Assess the diet of possums in the study site in a spatiotemporally explicit fashion in order to define preference for different food types;

- Analyse habitat selection using compositional analysis at Johnson's (1980) second and third order spatial scales, and at annual and bi-monthly temporal scales in order to define preference for different habitat types;

- Elucidate the relationships between resource parameters and possum utilisation of 0.5 ha cells with multiple and logistic regression of pooled and individual possums at Johnson's (1980) second and third order spatial scales, and at annual and bi-monthly temporal scales (resource parameters include species' abundance, forest structure, species diversity and combined abundance of preferred species as defined by diet selection analysis);

- Contrast the benefits and limitations of the different resource selection approaches used here.

5.2 Methods

The resource selection design used in this study is classified by Thomas and Taylor (1990) and Manly *et al.* (1993) as design III because individuals are used as the

sampling unit and resource use and availability are assessed for each individual. Type I designs derive a singular level of use of a resource for a population and relate it to a singular level of availibilty of that resource (Thomas and Taylor, 1990). Type II designs do likewise, but the singular level of use is pooled from levels of use measured on individuals (Thomas and Taylor, 1990). The type III design was used as it allows individual variation in selection to be examined and tested, can be extended for population inferences (Manly *et al.*, 1993), and avoids problems associated with pooling data (Schooley, 1994).

In recognition of the hierarchical nature of resource selection, analysis proceeded at multiple spatiotemporal scales. Spatial scale was considered at Johnson's (1980) second and third order selection level. These scales are likely to hold the most significant implications for the management of possums because they are congruent with the scales at which control and monitoring takes place. Temporal scale was considered at the bi-monthly and annual level in order to examine the change of habitat use in response to change in availability and demand. The six radio-tracking periods were combined to provide three seasons; March-May (3&5), July-September (7&9) and November-January (11&1). This was done to increase sample size for each season and to simplify analysis in order to provide more interpretable results (see discussion in Chapter 3).

All spatial analysis was carried out using ARCVIEW GIS 3.2a (ESRI, 2001).

5.2.1 Comparison of resource use and availability

Comparisons of use and availability are the most common and widely accepted form of resource selection analysis (Thomas and Taylor, 1990; Manly *et al.*, 1993; Erickson *et al.*, 2001). Comparisons of use and availability proceed at two scales within this study; diet selection and habitat selection.

5.2.1.1 Diet selection

Diet selection was elucidated by sampling possum diet and comparing it to plant species availability in the study site in order to obtain possums' preferences for each species.

5.2.1.1.1 Sampling

Trapping of possums occurred in April, August and December, 2002, coinciding with the seasons defined by the radio-tracking field work. Significant possum control had occurred within the study site by this time (Bygate, 2001), hence possum numbers were low. For this reason, Victor® no.1 leg-hold traps were only set in areas containing visible signs of possum activity. Traps were set on the ground adjacent to trees to which they were anchored with fencing staples; flour mixed with icing sugar was smeared along tree trunks to act as lure. Traps were checked as early as possible on the morning following setting and trapped possums were quickly killed. Stomachs were removed, placed in a labelled bag and were then frozen as soon as possible (usually two to four hours afterwards). Trapping was concluded once a target of approximately 20 stomachs had been collected for each trapping excursion. This number was chosen because it was believed that trapping more possums within the study site during the first trapping excursions would prevent satisfactory sample sizes being achieved in subsequent trapping excursions, given the low residual population (M. Bygate, pers. comm.). Sweetapple (2000) undertook analysis to determine suitable sample sizes for possum stomach analysis in *Nothofagus* forest and concluded that between 30 and 35 stomachs would provide adequate power to detect two-fold differences in means most of the time. However, vegetation variability constitutes a large component of the variability in diet and because vegetation variability will be accounted for in this study, adequate power in preference indices should be attained for samples of 20 stomachs per season.

Problems have been identified with using leg-hold traps to obtain samples in possum stomach contents analysis (Nugent *et al.*, 1997). Perhaps the most important is the continued digestion and mixing of food items in the stomach while the possum waits to be killed. It is recognised that the use of leg-hold traps in this study is not ideal; however, given financial and time constraints, the use of leg-hold traps was deemed

the most suitable method. Furthermore, the use of leg-hold traps to obtain stomach samples has been deemed adequate in other possum diet studies (Sweetapple, 2000).

5.2.1.1.2 Stomach content analysis

Stomach contents were analysed using the layer separation method proposed by Sweetapple and Nugent (1998). This method has been found to be advantageous over other techniques used for possum diet assessment for several reasons as follows: no correction need be made for digestive rate, survival of preparation process or area-to-weight ratios; non-foliage food types are accurately assessed; food items are readily identifiable (Sweetapple and Nugent, 1998). However, a limitation of this method is that mixed stomachs are not easily analysed (Sweetapple and Nugent, 1998).

Possum stomachs were thawed, weighed and cut along their greater curvature to reveal their contents. Layers were separated using a spoon, identified and placed onto labelled metal trays, which went into a drying oven at approximately 70°C for 24 h. Mixed layers had the ratio of constituents estimated by eye. Finally, dried samples were weighed and proportional consumption of food types was calculated using these dry weights.

Spatial representation of stomach contents was displayed using interpolation techniques. This method allows the value of a variable at a specific site to be estimated from the measured values of that variable at neighbouring sites (Partington, 1997). Interpolations were performed with the inverse distance weighted (IDW) method, which allows the relative importance of neighbouring values in the interpolation calculation to diminish with increasing distance (Watson and Philip, 1985). The nearest 20 neighbours were used to define point estimates for the five most highly consumed food types in the interpolations for all stomach samples combined. This method was used only as a general guide to where food items were obtained because it is recognised that possum capture site is not synonymous with feeding site, although the two are correlated.

5.2.1.1.3 Preference indices

Numerous indices devised to calculate food preferences have been proposed in the literature (Manly *et al.*, 1993), yet many of the most widely used indices give similar results when preferences are ranked (Lechowicz, 1982). Given the problems associated with measuring food selection, stating absolute preference calculated with preference indices is likely to overstate their accuracy (Norbury and Sanson, 1992). As such, use of preference ranks is recommended as they represent the critical aspect of relative preference without succumbing to the pitfalls associated with absolute preference estimation (Aebischer *et al.*, 1993).

Given Lechowicz's (1982) findings, the forage ratio (Ivlev, 1961) was chosen to calculate possum diet preferences because of its simplicity and is given by:

$$P_i = \frac{d_i}{f_i} \qquad \textbf{Equation 5.1}$$

where P_i is the forage ratio for food type i, d_i is the proportion of food type i in the diet and f_i is the proportion of food type i available.

An attempt was made to account for some of the variability involved with estimating availability by defining multiple spatial scales at which food species were available to each sampled possum. These were: areas represented by circles with areas of 0.5, 4.5, 12.5, 24.5 and 40.5 ha centred on capture locations; a concentric-weighted-ring method, also centred on capture locations; the study site.

The first set of areas represented those encompassed by one cell, 3×3, 5×5, 7×7 and 9×9 cells; these were defined in order to encapsulate the heterogeneity of food species distribution. The concentric-weighted-ring method was devised to incorporate movement parameters into the definition of food availability and was as follows: A circle of radius 500 m was centred on possums' capture location and was divided into 9 concentric rings and a central circle; Each ring was assigned a weight; the central circle was weighted as one and subsequent weights decreased by 0.1 outwards from the centre; Weights were applied to species' importance values by intersecting these rings with the vegetation map of the study site; species' importance values were multiplied by the areas of intersected polygons and assigned weights of those

polygons; Weighted importance values were then summed for each species and proportional abundance was calculated. In notational form this can be expressed as:

$$F_i = \frac{\sum_{p=1}^{m} v_i a_p w_p}{\sum_{p=1}^{m}\sum_{i=1}^{n} v_i a_p w_p} \qquad \textbf{Equation 5.2}$$

where F_i represents proportional availability of food species i, of which there are n; v_i represents the importance value of food species i, w_p represents weight and a_p represents the area of intersected polygon p, of which there are m.

Movement parameters are incorporated with this method in two ways; the extent of the outermost ring corresponds to the maximum measured nightly range of telemetered possums within the study site and the weights on rings seek to describe the decreasing likelihood of interception between possum and food item with increasing distance from capture location.

The study site was defined as the level of availability in order to make comparisons with other studies because this is the scale typically used in diet preference studies (van Vreede *et al.*, 1989; Forsyth *et al.*, 2002), especially with regard to possum diet preference (Owen and Norton, 1995; Nugent *et al.*, 1997; Cochrane *et al.*, 2003).

Fruits and flowers were not directly assessed within the study site, but their abundance was estimated by extrapolating from litterfall data presented by Nugent and Sweetapple (1997), collected in the Pureora Conservation Park, central North Island. This data was used because no more-suitable data was available. Extrapolations were made by multiplying species' abundance data in the study site by the ratio of fruits or flowers to foliage obtained from the Puroera litterfall data. Despite being derived from a different forest type, there is no reason to believe that ratios should exhibit large differences between sites. Furthermore, this method is unlikely to yield significant biases because diet preferences will be presented as ranks.

Diet preferences were calculated on vascular plant species for each collection (April, August and December) and overall. Analyses of diet preference using stomach contents are disadvantaged by its destructive nature; stomach contents represent an

instantaneous sample of diet and, as such, average consumption of food items by an individual cannot be ascertained. This is likely to lead to frequent consumed values of zero for food items because possums' consumption is limited to a few food types each night (Nugent *et al.*, 1997; Cochrane *et al.*, 2003). As such, non-consumption may reflect either selection or the lack of realistic availability.

Either way, zero values lead to spurious forage ratios. Substitution of very small values for zero consumed values may alleviate this problem as we can assume that, because sampling is instantaneous, possums may not have had a realistic opportunity to eat certain food items. This effect takes on more significance when it is considered that possums may have been trapped early in the night. Used values equivalent to zero were substituted with values an order of magnitude less than the smallest measured consumption value for forage ratio calcualtions.

Given the limitations of instantaneous diet assessment, a further method of calculating preference of the sample possums was developed; forage ratios of food types were averaged only across individuals that consumed them (hereafter termed the 'overall conditional mean'). The main advantage of this method lies in the certainty that a food type was available to all the possums for which the average forage ratio is given. In contrast, when averages are calculated for all possums we can not determine whether a food item was non-consumed through selection or lack of availability.

Once diet preferences were estimated they were used to ascertain the relationship between home range size and forage quality. This was achieved by calculating the average abundance of the top ten preferred species, as defined by the overall sample for all scales, within the cells contained by each possum's home range. Additionally, averages were calculated with natural log compressions of individual species to decrease the importance of abundant species. These values were then modelled against the dependent variable of home range size using multiple regression to ascertain whether there were any significant relationships between home range size and forage quality as defined by diet preference.

5.2.1.2 Habitat selection

Habitat selection was tested by comparing the use of classified habitat types to their availability within the study site at two spatial scales and two temporal scales in order to assess possums' preference for these habitat types.

5.2.1.2.1 Habitat classification

The vegetation types derived in Chapter 4 were taken as the habitat types to be analysed. It is important to realise that the forest structure and composition heterogeneity within the forest was relatively low, and most accurately represented a continuum of vegetation characteristics, as opposed to a habitat mosaic with obvious discontinuities between distinct vegetation types. For this reason the boundaries between the forested habitat types were somewhat arbitrarily placed and were likely to be unrecognisable to possums. In contrast, the boundaries between vegetation type one and the closed forest vegetation types were very distinct and were likely to be highly recognisable by possums.

5.2.1.2.2 Use of habitat types

At the second order selection level, the composition of the home range is tested against the composition of the wider study area (Aebischer *et al.*, 1993). Habitat type composition of home range was evaluated by intersecting the kernel-estimated home range shapefiles with the habitat type shapefiles in Arcview GIS 3.2a. Use was then taken as the proportions of each habitat type within each individual's home range.

At the third order selection level, the process of interest is the use of habitat types within the home range. Typically, design III habitat selection studies use the proportion of radio-locations within specific habitat types as the measure of use at this scale, but seldom report the effect of telemetry error on the likelihood of correct allocation of radio locations to habitat types (Warnock and Takekawa, 1995; Staus, 1998; Lariviere and Messier, 2000; Lurz *et al.*, 2000; Revilla *et al.*, 2000; Valenzuela and Ceballos, 2000; Gabor *et al.*, 2001; Ratcliffe and Crowe, 2001). This method was not applicable to this study because cell references frequently included multiple habitat types, and made it difficult to assign radio locations to individual habitat types. As a solution, proportional habitat use within home range was estimated using spatial

manipulations in Arcview GIS 3.2a. This was achieved by intersecting probability contours (5, 15, 25, 35, 45, 55, 65, 75, 85, and 95 %) from individual home ranges with habitat type shapefiles, then summing the allocated habitat use areas across probability contours, and dividing these summed use areas by the total summed area for each individual. This process can be put into notational form:

$$U_i = \frac{\sum_{j=1}^{m} a_{ij}}{\sum_{j=1}^{m}\sum_{i=1}^{n} a_{ij}} \qquad \textbf{Equation 5.3}$$

where U_i represents the proportion of area in habitat type i, a_{ij} represents the area of the polygon created by intersecting probability contour j and habitat type i, and m and n represent the number of probability contours and habitat types respectively.

This method effectively weighted the use of habitat types by the utilisation distribution as represented by the probability contours and allowed differentiation between the levels of habitat use within the home range. This use of kernel-estimated home ranges in a GIS environment to calculate habitat use has been shown in other studies to be as effective as telemetry point allocation methods (e.g. Kernohan *et al.*, 1998). In addition, this method reduces the effect of telemetry error, is insensitive to autocorrelation problems, and is representative of the complete utilisation by an animal as opposed to sub-sampling from the overall movement trajectory (Kernohan *et al.*, 1998).

5.2.1.2.3 Habitat type availability

Habitat availability at the second order selection scale is defined as habitat type proportions within the extent of the study area, and is commonly specified arbitrarily (Johnson, 1980; Porter and Church, 1987; Aebischer *et al.*, 1993). To make this definition of availability more objective, the study area was bounded by the maximum range length (750 m) from core areas of the outermost telemetered possums, or the Upper Grey River; whichever was the shortest distance. This definition incorporates possum-specific biological parameters such as reluctance to cross major waterways (Brockie *et al.*, 1989; Cowan and Rhodes, 1993; Rose *et al.*, 1993; Pekelharing *et al.*, 1998b) and potential of movement, however, it must be noted that this definition remains an arbitrary one.

The typical definition of habitat availability at the third order selection scale in design III studies is that of home range extent (Warnock and Takekawa, 1995; Staus, 1998; Lariviere and Messier, 2000; Lurz *et al.*, 2000; Revilla *et al.*, 2000; Valenzuela and Ceballos, 2000; Gabor *et al.*, 2001; Ratcliffe and Crowe, 2001). Availability then becomes the proportion of a given habitat type within the home range.

5.2.1.2.4 Statistical analysis

The use of habitat proportions introduces statistical problems because they are not independent (unit-sum constraint: all components sum to one) and, therefore, increase the likelihood of Type 1 errors in analyses (Aebischer *et al.*, 1993). Compositional analysis avoids the dependence problem by transforming habitat proportions into log-ratios, thereby rendering the units of analysis linearly independent of each other (Aebischer *et al.*, 1993; Elston *et al.*, 1996). Log-ratios are constructed by arbitrarily choosing one of n habitat types as the denominator of habitat proportion ratios and then taking the natural log of this ratio. The habitat type chosen as the denominator is not included as a distinct log-ratio because it is included implicitly in all other log-ratios, providing n-1 log ratios in total. Results from analysis of these log-ratios are independent of the choice of denominator (Aebischer *et al.*, 1993).

Compositional analysis is defined as the application of statistical procedures to these log-ratios (Aitchison, 1986). The most useful of these is the multivariate analysis of variance (MANOVA) because it allows the difference between corresponding use and availability log-ratios (the residual log-ratio) for habitat types (n-1) and individuals to be analysed simultaneously. Selectivity is established by testing log-ratio differences for significant deviation from zero using the Wilk's lambda statistic. Following selectivity testing, a ranking of the habitat types by preference can proceed. Differences in selectivity between habitat types can be tested with the t statistic. All compositional analysis was performed in SAS (SAS Institute Inc., 2000) using the program BYCOMP.SAS (Ott and Hovey, 1997).

Calculations of home ranges for use in resource selection analysis did not incorporate the location of den sites. This approach was adopted for several reasons:

- potential den sites were surplus to demand because population density was low and large *Nothofagus* trees provided numerous sites for dens in bole cavities and underneath root plates;
- den sites appeared to be randomly distributed throughout the study area and did not appear to be linked to any landform or vegetation type (Figure 3.16);
- den sites do not necessarily correlate with foraging areas (Ward, 1978);
- of all behaviour, possums are most likely to exhibit resource selection in relation to foraging not denning.

It is difficult to know if possums are engaging in foraging behaviour right up to the point of denning or immediately following emergence from the den. However, other research indicates that feeding behaviour constitutes only a small proportion of overall behaviour (MacLennan, 1984), which suggests that possums are likely to be satiated long before entering the den at the end of a night. Furthermore, feeding activity is likely to initiate more than two hours following emergence from the den site (MacLennan, 1984) and, as such, is likely to coincide with the first active fix in each tracking night. Although travel to and from den sites may have potential implications for resource selection, they are likely to be superficial when compared to those associated with general active behaviour.

Zero values for habitat proportions required adjustment because such values for the numerator or denominator of a ratio lead to an invalid ratio or log of that ratio. Adjustments were undertaken within guidelines specified by Aebischer *et al* (1993). Habitat types that were available but unused had the zero value substituted with a number that was an order of magnitude smaller than the smallest measured used-habitat proportion. This created valid log-ratios without seriously altering the essence of selection embodied within them. However, when a habitat type was not available at the third order selection scale and was, consequently, unused, the invalid residual log-ratio was replaced with the mean of all non-missing values for that log-ratio. This allowed animals affected by this situation to be retained in the overall analysis without overly biasing analysis of the habitat type that was unavailable. However, when this situation applied to most animals the unavailable habitat type was omitted from the analysis.

5.2.2 Modelling

Modelling was used as an alternative method for assessing resource selection at Johnson's second and third order selection scale (1980) because it has the advantage of not being reliant on habitat classification.

5.2.2.1 Use of space

The units for all modelling of resource selection were taken to be the 0.5 ha cells used to record the locations of radio-tracked possums. The level of use of these cells was calculated in the same way as for habitats (Equation 5.3).

5.2.2.2 Resource variables

All variables used in modelling analysis were derived from the vegetation assessment outlined in Chapter 4. First level variables were taken as the importance values of all vascular plant species within the study site. Second level variables were constructed as composites of first level variables. They were: diversity indices (species richness and Shannon diversity index), tier importance values (the sum of all species' importance values within each tier), total importance value (an index of overall biomass), functional group classifications (grass and herbs, ferns, non-seral shrubs, seral shrubs, and lianes)[2], and diet preference scores (summed importance values as well as the natural-log-compressed importance values[3] of the top 10 ranked preferred species for each season and overall).

Site variables such as aspect, slope or drainage were not assessed because the scale of their maximal heterogeneity within the study site is far finer than the 0.5 ha scale of the grid cells and their overall heterogeneity within the study site is minimal. Regardless, much of the information that these variables contain is also implicitly represented by vegetation heterogeneity. This contention is supported by a study

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[2] Canopy species were not included due to the overwhelming dominance of *N. fusca* and *N. menziesii*. For a full account of all resource variables see Appendix 2 and Appendix 3.

[3] Importance values were natural-log-transformed to alleviate the influence of extremely abundant species.

conducted at nearby Mt Harata that identified strong correlations between vegetation communities and landform and soil types (Stewart *et al.*, 1993).

For practical purposes resource availability can be defined as the quantity available to an animal (Manly *et al.*, 1993) and is represented in this study in terms of importance value, which is an index of biomass or density (Chapter 4). Abundance is but one component of resource availability (Porter and Church, 1987; Orians and Wittenberger, 1991; Otis, 1998; Wilson *et al.*, 1998; Rosenberg and McKelvey, 1999), yet it is the most important one in this study because wild possums do not exhibit strong territoriality (Green, 1984), predation is uncommon in the study site and spatially explicit analyses mitigate the importance of resource distribution.

5.2.2.3 Statistical analysis

Modelling was performed at scales broadly analogous to Johnson's (1980) second and third order spatial scales as well as the annual and bi-monthly temporal scales using multiple and logistic regression in SAS (SAS Institute Inc., 2000). The second order selection scale was approximated by categorising individual use of cells into used/unused for all cells within the study site followed by modelling against the levels of resource variables. The third order selection scale was approximated by modelling the level of cell use against the level of resource variables within the home range only. Logistic regression was used at the second order selection scale and multiple regression was used at the third order selection scale.

Population modelling was performed on pooled data for annual and bi-monthly data sets using multiple regression. It is recognised that pooling observations has many limitations (Schooley, 1994), yet the influence of non-random sampling of possums can be somewhat controlled by taking the average use of cells by possums, as opposed to pooled use, and by excluding unused cells from analysis. This analysis is designed to test for population-wide trends in correlations between use of cells and cell properties.

Models were selected using the same approach regardless of regression technique. This approach involved multiple steps as follows:

1. Stepwise selection was used to identify potential model variables based on their P value;
2. Outliers greater than three standard deviations (Morrison *et al.*, 1992) from the mean were discarded;
3. Highly correlated variables were separated by removing the ones with the highest P values;
4. Regression was re-run;
5. Variables with P values greater than 0.05 were removed;
6. Regression was re-run until all variables had P values less than 0.05.

Principle components analysis was not deemed necessary because only a few of the resource variables were highly correlated and such analysis does not lend itself to clear interpretation when numerous variables are used; interpretation requires subjective assessment of variable coefficients within principle components deemed significant (Morrison *et al.*, 1992) and therefore becomes more convoluted with increasing numbers of variables.

5.3 Results

5.3.1 Diet selection

Stomachs were collected from 62 possums trapped within the study site; 19 stomachs were collected in April, 23 in August and 20 in December 2002. Traps were set in transects along the escarpment beside the northern section of the road, on the terrace edge above the swamp, along the true left of the central creek, and along the intersection of the base of the hill and the southern terrace. Traps were only set in these areas because little possum sign was seen elsewhere.

Figure 5.2: Capture locations of possums used for diet analysis.

As suspected, possums became increasingly difficult to trap on subsequent excursions and it is unlikely that a significantly larger sample could have been achieved without a dramatic increase in resources and time. The distribution of trapped possums correlates highly with the areas utilised by the radio tracked possums (Figure 5.2). Of the 62 possums caught, 33 were female and 29 were male. The average weight of females was 2.6 ± 0.1 kg (mean ± standard error) and the average weight of males was 2.8 ± 0.1 kg. No significant difference was detected between these weights (F value = 0.966, P value = 0.33). The average weight of all possums was 2.7 ± 0.1 kg including stomach and 2.6 ± 0.1 kg without, which is similar to the average weight for the radio-tracked possums (2.6 ± 0.2 kg).

Five stomachs contained too little food to be analysed; one in April and four in August. Mixed layers were present in one stomach in August, two in April and four in December.

Possums consumed, on average, 3.3 ± 0.3 food types per night. However, variation in food item consumption did exist between the seasons with 3.2 ± 0.5 types consumed

per night in the April sample, 2.6 ± 0.3 types consumed per night in the August sample and 4.1 ± 0.5 types consumed per night in the December sample. The difference between the August and December samples was significant (*F* value = 6.11, P value = 0.02). Associated with this decrease in the number of food items consumed in August was an increased reliance on staple diet constituents (Table 5.1). In total, 46 food types were identified from the overall diet sample. Table 5.1 illustrates how use of an overall measurement of consumption underestimates the average contribution of the most highly consumed food types amongst seasons.

Table 5.1: Cumulative percentage composition of the most abundant food types within possum diet. The column labelled 'overall' represents the cumulative sum of the most highly consumed food types following averaging amongst seasons, whereas the column labelled 'mean' represents the mean of the cumulative sums themselves.

Rank abundance	Season				
	Apr	Aug	Dec	Mean	Overall
1	15.7	30.9	16.4	21.0	16.1
2	27.5	47.8	32.3	35.9	24.6
3	38.9	62.7	45.4	49.0	31.8
4	49.5	71.9	55.6	59.0	38.3
5	59.6	80.7	63.0	67.7	44.4

Possums within the study site primarily consumed tree foliage; however, non-foliar food types such as wood, litter and fungi comprised greater than a quarter of overall diet (Table 5.2). Compared to woody plant foliage, herbaceous and grass species were relatively uncommon in the diet sample. Considerable variation in diet was displayed between the seasons, especially in the consumption of flowers and fungi; flowers were only consumed in summer and fungi were uncommon in winter diet. Invertebrates comprised a large percentage of winter diet, but were unimportant in other seasons. Fruits were eaten throughout the year with peak consumption occurring in winter. When consumed, fruit, flowers, fungi and invertebrates commonly dominated the stomach sample. Approximately 40 % of overall possum diet was likely obtained from the ground, as this is the percentage food items other than those provided by trees and shrubs in the diet.

Of all the food types, *Weinmannia racemosa* foliage was clearly consumed most frequently and in the greatest quantities (Table 5.3). The importance of *Weinmannia racemosa* is further highlighted when it is considered that while *Weinmannia racemosa* foliage consumption was low in December, *Weinmannia racemosa* flower consumption was high. Fungi and litter frequently occurred together in high abundance within stomach layers, suggesting that the litter was consumed incidentally. A similar relationship existed between insect larvae and litter. Fungi were consumed in similar quantities to foliar food types such as *Rubus cissoidies*, *Fuchsia excorticata* and *Neomyrtus pedunculata*. Insect larvae formed a significant part of winter diet for the sampled possums. It is interesting to note that possums deemed it worthwhile to consume large amounts of litter and debris in order to obtain these larvae, which suggests that these food items are highly sought after.

Table 5.2: Diet constituents by food type.

Food type	Mean % dry weight			
	April	August	December	Overall
Tree foliage	21.44	39.65	18.19	26.94
Wood/litter	13.72	10.77	20.44	14.86
Fungi	13.24	0.31	23.22	11.85
Liane foliage	21.82	9.22	0.51	10.29
Shrub foliage	15.22	6.22	5.48	8.78
Fruit	7.18	14.89	3.00	8.59
Invertebrates	0.02	13.81	1.67	5.54
Flowers	0.00	0.00	11.38	3.73
Herbs/grass	2.08	0.09	8.11	3.34
Other	3.80	5.04	0.53	3.17

Table 5.3: Diet constituents by species. Constituents are represented as a single food type if they occurred together in a layer. Numbers in parenthesis indicate the frequency of consumption. (frt) = fruit and (flwr) = flowers.

Diet constituents	Mean % dry weight			
	April	August	December	Overall
Woody species				
Weinmannia racemosa	15.71 (6)	30.85 (12)	0.36 (1)	15.64 (19)
Rubus cissoides	10.06 (5)	9.22 (3)	-	6.43 (8)
Fuchsia excorticata	1.16 (2)	-	16.42 (7)	5.86 (9)
Neomyrtus pedunculata	11.46 (6)	0.82 (1)	5.00 (1)	5.76 (8)
Carpodetus serratus (frt)	-	14.89 (6)	-	4.96 (6)
Muehlenbeckia australis	11.76 (7)	-	0.51 (2)	4.09 (9)
Weinmannia racemosa (flwr)	-	-	10.16 (4)	3.39 (4)
Metrosideros umbellata	-	8.80 (2)	-	2.93 (2)
Pseudowintera colensoi (frt)	6.70 (4)	-	-	2.23 (4)
Raukaua simplex	-	4.48 (1)	0.48 (1)	1.65 (2)
Peraxilla tetrapetala	4.57 (1)	-	-	1.52 (1)
Raukaua anomalous	3.76 (2)	0.60 (2)	-	1.45 (3)
Aristotelia serrata (flwr&frt)	-	-	2.44 (2)	0.81 (2)
Raukaua simplex (frt)	-	-	1.78 (5)	0.59 (5)
Aristotelia serrata	-	-	1.36 (2)	0.45 (2)
Coprosma rhamnoides (frt)	0.48 (1)	-	-	0.16 (1)
Coprosma propinqua	-	0.32 (1)	-	0.11 (1)
Herbs				
Cirsium spp.	-	-	2.65 (4)	0.88 (4)
Trifolium repens	-	-	1.85 (4)	0.62 (5)
Ranunculus spp.	-	0.03 (1)	1.32 (2)	0.45 (3)
Nertera villosa	0.56 (2)	0.00 (1)	0.73 (3)	0.43 (6)
Nertera depressa	-	0.06 (2)	1.08 (4)	0.38 (6)
Epilobium spp.	0.76 (1)	-	-	0.25 (1)
Lotus pedunculata	0.38 (1)	-	-	0.13 (1)
Other				
Fungi/Litter	10.56 (7)	-	15.89 (7)	8.82 (14)
Larvae/Litter	-	16.92 (8)	3.26 (1)	6.72 (9)
Fungi	5.34 (3)	0.31 (1)	13.12 (5)	6.26 (9)
Litter	5.82 (4)	2.31 (3)	8.72 (7)	5.61 (14)
Sooty mould	2.96 (1)	5.04 (2)	0.44 (1)	2.81 (4)
Fungi/wood	2.30 (1)	-	4.31 (1)	2.20 (2)
Larvae	0.02 (2)	5.35 (6)	0.01 (1)	1.79 (9)
Wood/litter/fungi	4.43 (1)	-	-	1.48 (1)
Liverwort	0.84 (1)	-	-	0.28 (1)
Ferns				
Blechnum procerum	-	-	7.44 (4)	2.48 (4)
<0.1%				
Hypochoeris radicata	-	-	0.24 (1)	0.08 (1)
Cardamine spp.	0.19 (1)	-	-	0.06 (1)
Rumex acetosa	0.19 (1)	-	-	0.06 (1)
Unidentified grasses	-	-	0.16 (1)	0.05 (1)
Bryophyte	-	-	0.08 (2)	0.03 (2)
Hydrocotyle spp.	-	-	0.06 (2)	0.02 (2)
Nothofagus fusca	-	-	0.05 (1)	0.02 (1)
Acaena spp.	-	-	0.03 (2)	0.01 (2)
Unidentified invertebrates	-	-	0.02 (2)	0.01 (2)
Coleoptera	-	-	0.02 (1)	0.01 (1)
Blechnum penna-marina	-	-	0.02 (1)	0.01 (1)

Some of the wood and sooty mould consumption may be attributable to possums attempting to eat lure smeared on trapping trees rather than the merits of these 'food' types. Of all the fruit present within the study site, the fruit of *Carpodetus serratus* was the most highly consumed, followed distantly by that of *Pseudopanax colensoi*. *Aristotelia serrata* fruit was only consumed in conjunction with flowers. Despite the high occurrence of *Carpodetus serratus* fruit in the diet, none of its foliage was detected. Fur and dirt was recorded in the diet, yet it is likely that they were ingested through grooming so it was deemed inappropriate to include them as food types. No evidence was found to suggest that sampled possums had eaten birds, bird eggs or mammals. The distribution of the five most frequently consumed food types is given in Figure 5.3, Figure 5.4, Figure 5.5, Figure 5.6 and Figure 5.7.

Table 5.4 and Table 5.5 indicate the effect of the definition of availability and the effect of season on diet preference analysis. The greatest variability within rank preferences was attributable to season and the method with which individual preference was averaged. All three seasons were consistent across spatial scales for the most preferred food types, they were: *Muehlenbeckia australis* foliage in April, *Carpodetus serratus* fruit in August and *Fuchsia excorticata* foliage in December. Most species displayed inconsistency in preference across season. The exceptions were: *Rubus cissoidies* (third in April, second in August), *Weinmannia racemosa* (fifth in April, third in August), *Neomyrtus pedunculata* (fourth in April, ninth in August, eighth in December), *Nertera depressa* (seventh in August, sixth in December), and *Ranunculus* spp. (eighth in August, tenth in December). Congruence between spatial scales was most consistent between 3×3 cells, 5×5 cells, 7×7 cells, 9×9 cells and the concentric weighted ring definition. The most frequently incongruent scale was the study site.

Overall, the most preferred food type was *Fuchsia excorticata* foliage, followed by *Carpodetus serratus* fruit (Table 5.5). However, when preferences were averaged for only those possums that consumed certain food types *C. serratus* fruit was found to the most preferred. Indeed, there was no congruence between preference ranks obtained by straight averaging and conditional averaging across possums.

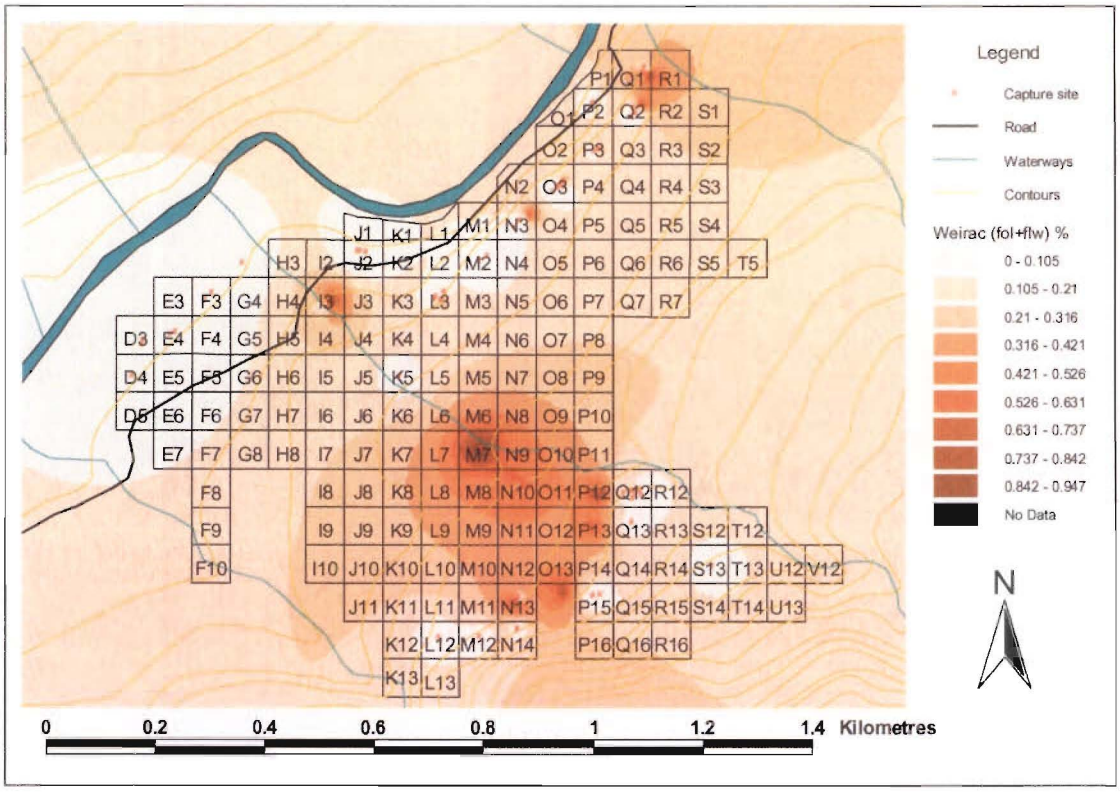

Figure 5.3: Interpolated surface representing the distribution of *Weinmannia racemosa* within possum diet.

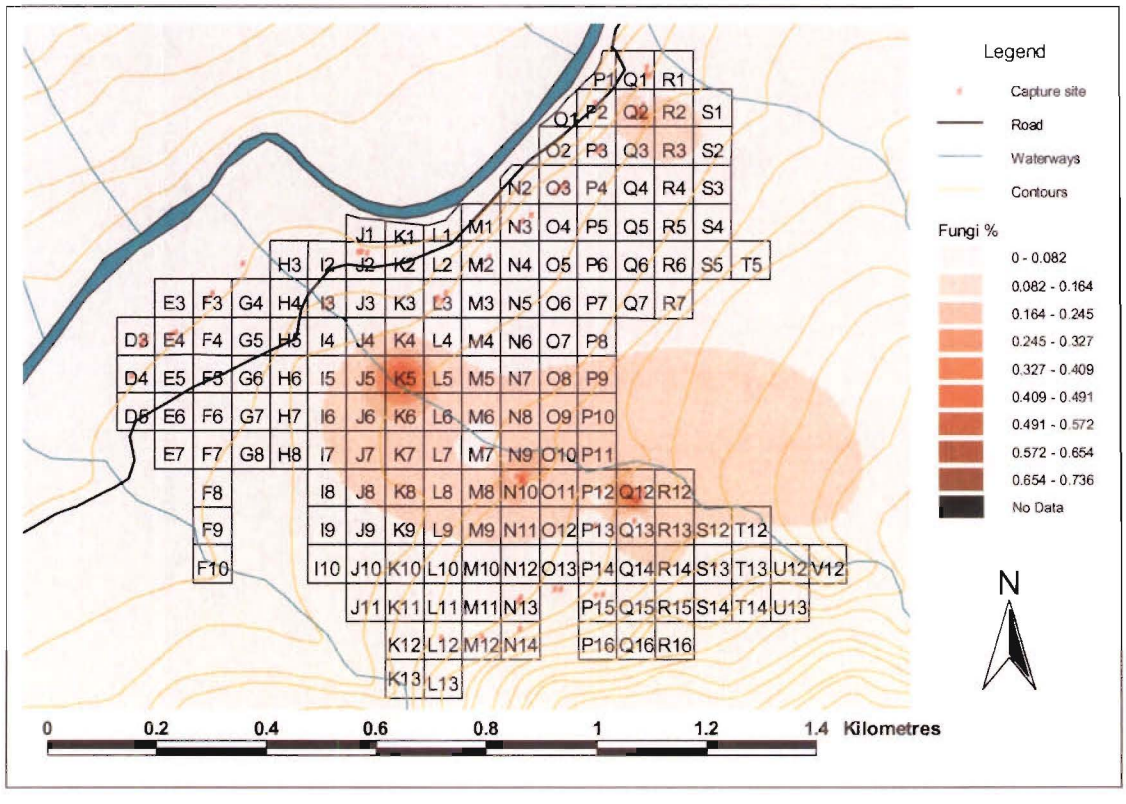

Figure 5.4: Interpolated surface representing the distribution of fungi within possum diet.

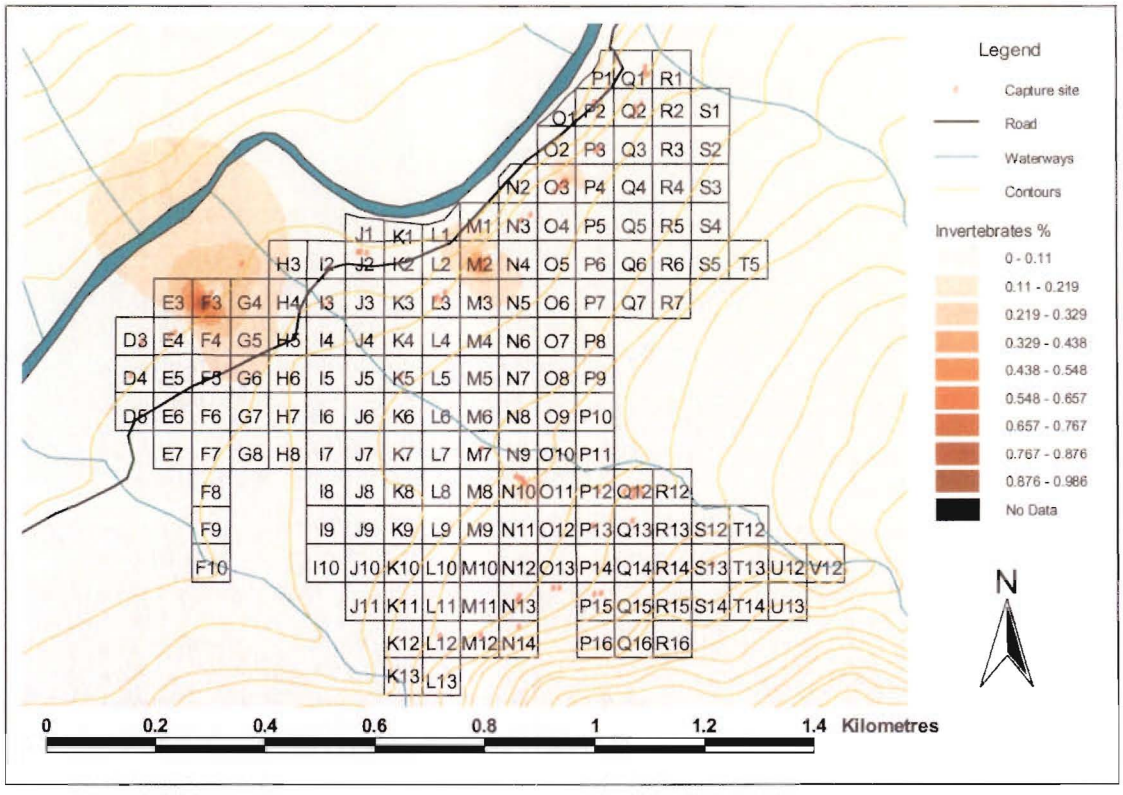

Figure 5.5: Interpolated surface representing the distribution of invertebrates within possum diet.

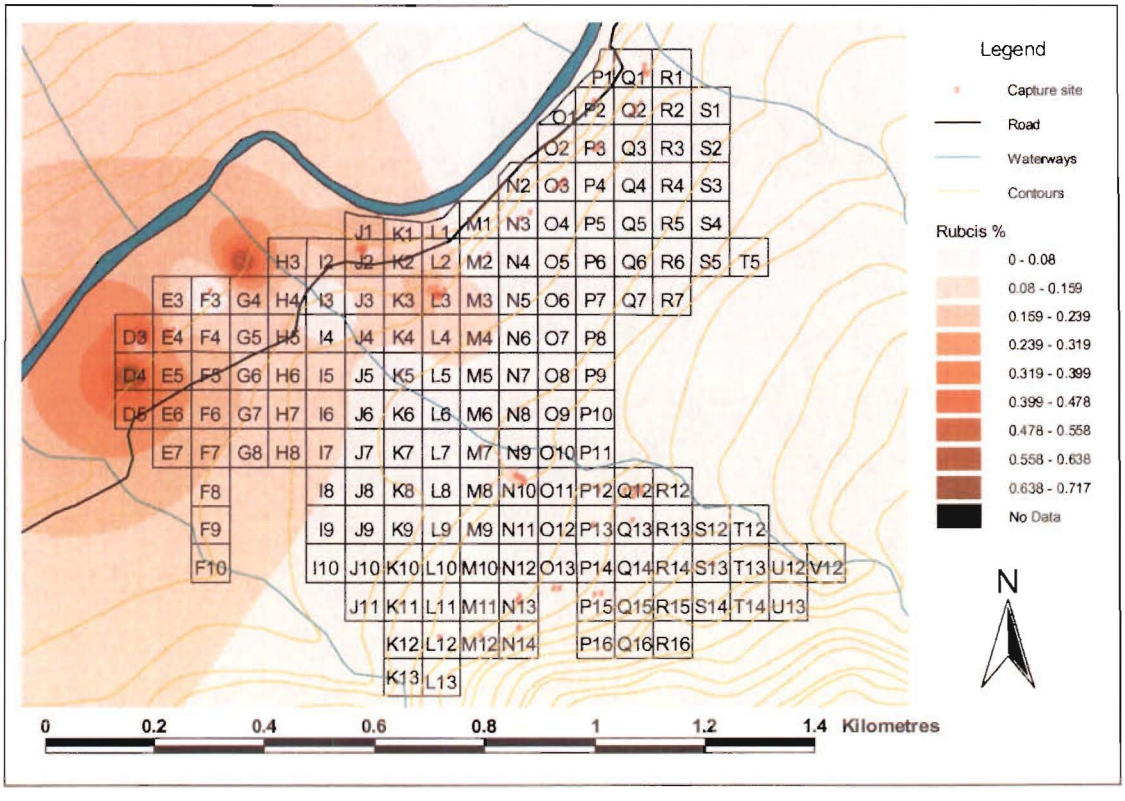

Figure 5.6: Interpolated surface representing the distribution of *Rubus cissoides* within possum diet.

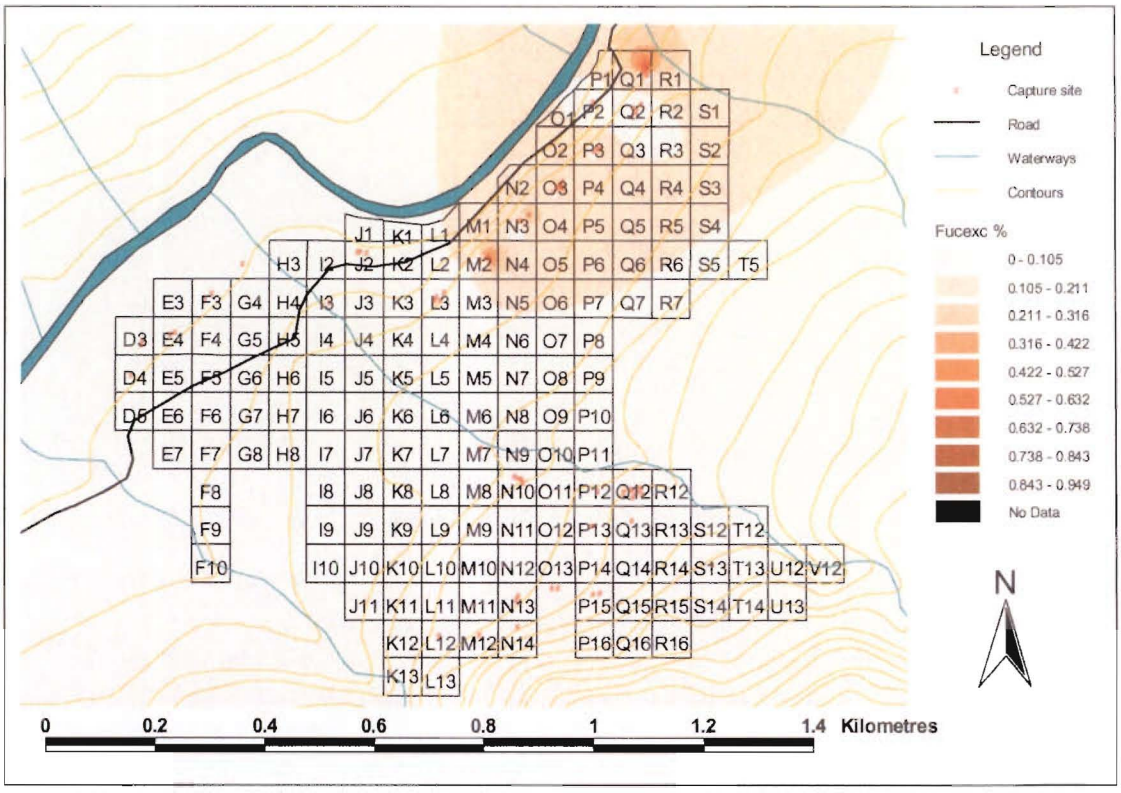

Figure 5.7: Interpolated surface representing the distribution of *Fuchsia excorticata* within possum diet.

Possums caught in areas of abundant *Weinmannia racemosa* did not necessarily consume large amounts of it, but possums that did consume large amounts of it were typically caught in areas with high *W. racemosa* abundance (Figure 5.3). Fungi were most highly consumed by possums caught within the central part of the study area (Figure 5.4). Invertebrates were only consumed in high to moderate abundance by one possum caught on the lowest section of the terrace and by several possums caught on the escarpment above the road (Figure 5.5). *Rubus cissoides* was only consumed highly by possums caught in western areas of the study site away from the hillside (Figure 5.6). The high consumption of *Rubus cissoides* by the possums caught in cells D3 and D4 suggest that they had fed elsewhere as no *R. cissoides* was observed in these cells (Chapter 4). Congruent with its distribution, *Fuchsia excorticata* was only consumed by possums caught along the escarpment above the northern section of the road (Figure 5.7). Obviously these possums were caught after they had fed at the roadside.

Table 5.4: Rank preference of food types for all seasons (1 is most preferred, only top ten food types shown for each scale). Food type names are the first three letters of the generic name followed by the first three letters of the specific name, (frt) = fruit and (flwr) = flowers.

Food type	Rank preference																											
	April								August								December											
	1*	2	3	4	5	6	7	M	1	2	3	4	5	6	7	M	1	2	3	4	5	6	7	M				
Carser(frt)									1	1	1	1	1	1	1	1												
Mueaus	1	1	1	1	1	1	1	1																				
Psecon(frt)	3	2	2	2	2	2	2	2																				
Fucexc	6	6	6	6	6	6	5	6									1	1	1	1	1	1	1	1				
Rubcis	2	3	3	3	3	3	3	3	2	2	2	2	3	2	3	2												
Blepro																	2	2	2	2	2	2	2	2				
Weirac	5	5	5	5	5	5	7	5	4	3	3	3	2	3	2	3												
Rausim(frt)																	5	5	5	5	5	5	5	5				
Cirspp																	3	3	3	3	3	3	3	3				
Coppro									7	6	6	6	7	6	6	6												
Rausim									5	5	5	5	5	5	5	5												
Metumb									3	4	4	4	4	4	4	4												
Neoped	4	4	4	4	4	4	4	4	6	9	9	9	9	9	10	9	9	8	8	8	8	8	7	8				
Trirep																	4	4	4	4	4	4	4	4				
Pertet	7	7	7	7	7	7	6	7																				
Weirac(flwr)																	7	7	7	7	7	7	8	7				
Nerdep									8	7	7	7	6	7	7	7	6	6	6	6	6	6	6	6				
Nervil	9	8	8	8	8	8	8	8									9	9	9	9	9	9	10	9				
Ranspp									9	8	8	8	8	8	9	8	8	10	10	10	10	10	9	10				
Lotped	10	9	9		9	9	9	9																				
Rauano	8				9	10			10	10	10	10	10	10	8	10												
Cardsp	10	10	10		10	10		10																				

*spatial scales: 1 = 1 cell, 2 = 3×3 cells, 3 = 5×5 cells, 4 = 7×7 cells, 5 = 9×9 cells, 6 = study site, 7 = concentric weighted ring, M = mode preference rank (where tied, given to the food type with the most frequent ranking).

Table 5.5: Rank preference of food types overall (1 is most preferred, only top ten food types shown for each scale). Food type names are the first three letters of the generic name followed by the first three letters of the specific name, (frt) = fruit and (flwr) = flowers.

Food type	Rank preference															
	Overall								Overall conditional mean							
	1*	2	3	4	5	6	7	M	1	2	3	4	5	6	7	M
Fucexc	1	1	1	1	1	1	1	1	4	7	7	7	5	5	5	5
Carser(frt)	3	2	2	2	2	2	2	2	2	1	1	1	1	1	1	1
Rubcis	2	3	3	3	3	3	4	3	5	4	6	8	8	8	9	8
Mueaus	4	4	4	4	4	4	3	4		10	10					
Psecon(frt)	7	5	5	5	6	5	5	5	3	2	2	2	2	2	2	2
Weirac	6	7	6	6	5	6	7	6								
Neoped	5	6	7	7	7	7	6	7								
Trirep	8	8	8	8	9	9	9	8		9	9	9	9	9	10	9
Nerdep	10	9	10	9	8	8	8	9								
Cirspp	9	10	9	10	10	10	10	10	7	3	3	4	4	4	6	4
Ariser(flwr&frt)									9	5	4	3	3	3	3	3
Blepro									8	6	5	5	6	6	8	6
Rausim									6	8	8	6	7	7	7	7
Metumb									1			10	10	10	4	10
Ranspp									10							

*spatial scales: 1 = 1 cell, 2 = 3×3 cells, 3 = 5×5 cells, 4 = 7×7 cells, 5 = 9×9 cells, 6 = study site, 7 = concentric weighted ring, M = mode preference rank (where tied, given to the food type with the most frequent ranking).

Rank preferences were used to define forage quality by summing the abundances of the top ten palatable species within each cell. Following modelling of forage quality against home range size, a significant relationship was detected between home range size and forage quality at two scales; July/September and annual (Table 5.6). The only independent variable that provided significant models was the natural-log-compressed abundance of the top ten preferred species calculated over all seasons. These models indicate that increasing forage quality is related to decreasing home range size. However, the model r^2 values indicate that the index of forage quality used explains only 30 – 40 % of the variation in home range size.

Table 5.6: Regression parameters for home range size versus forage quality given for scales in which a significant relationship was identified.

Temporal Scale	Model ANOVA					
	Adj. R^2	F value	Pr > F			
7&9	0.3778	7.07	0.0261			
Annual	0.3196	6.17	0.0324			
	Model parameter estimates					
	Variable	DF	Parameter estimate	Standard error	t value	Pr > |t|
7&9	Intercept	1	76126	10078	7.55	<.0001
	Ln(Overall)	1	-10096	3796.65	-2.66	0.0261
Annual	Intercept	1	140149	24957	5.62	0.0002
	Ln(Overall)	1	-22992	9259.07	-2.48	0.0324

5.3.2 Habitat selection

5.3.2.1 Habitat classifications

Although there is very little difference in forest structure between the forested habitat types, there are relatively major differences in species composition, and in particular, preferred species composition. Descriptions of vegetation types are given in detail in Chapter 4.

5.3.2.2 Compositional analysis

No significant overall selection was detected at any scales, although the significance level was approached at two scales; March/May and Annual at the third order selection scale (Table 5.7).

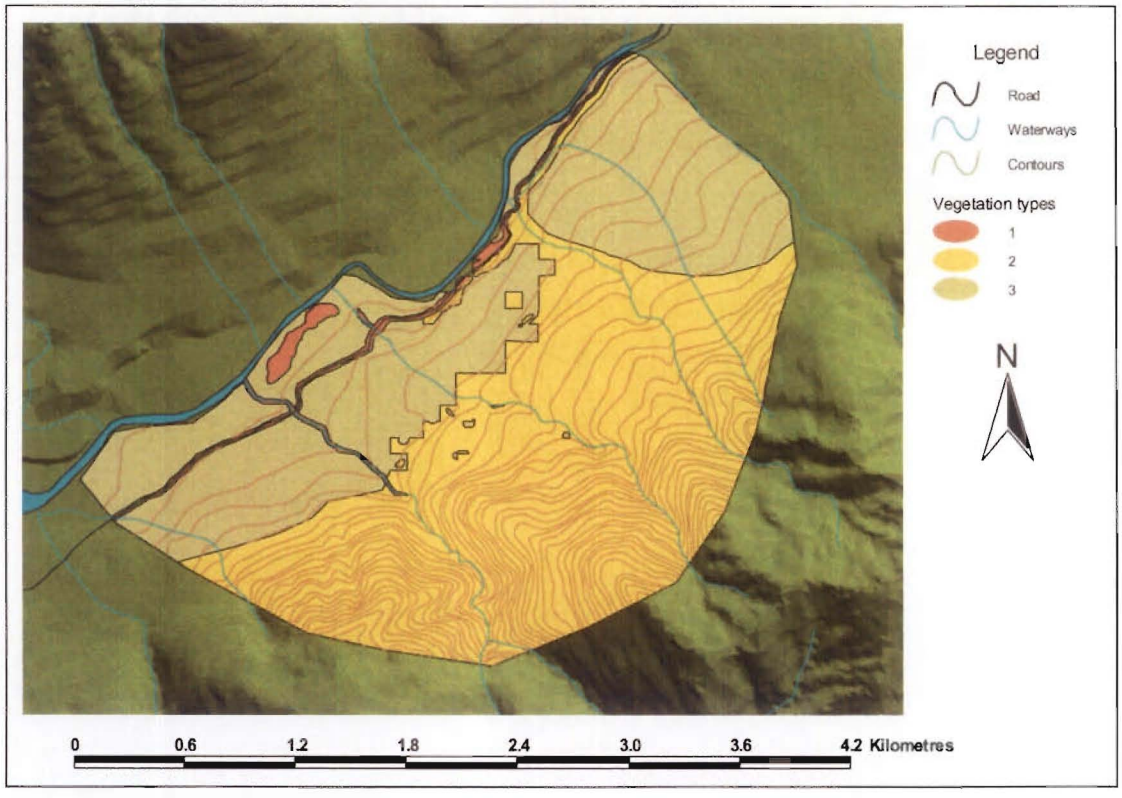

Figure 5.8: Vegetation types within the wider study area. Angular borders between vegetation types represent cell boundaries.

Table 5.7: Results of compositional analysis to test for significant selection (i.e. log ratio differences are significantly different from zero). Numbers shown as temporal scales represent aggregated months.

Temporal scale	Second order selection		Third order selection	
	F value	P value	F value	P value
3&5	0.35	0.716	3.13	0.088
7&9	0.54	0.601	2.72	0.119
11&1	1.35	0.329	1.59	0.280
Annual	0.30	0.751	3.77	0.060

Despite the lack of evidence showing the occurrence of overall selection between habitat types, possums did exhibit some significant differences in preference between habitat types. These occurred at all of the subsets of the third order selection scale, except for the November/January subset. In all cases, habitat type three was

significantly more preferred than one or both of the other habitat types. Nevertheless, it must be recognised that these results were based on pairwise comparisons between averaged log-ratio differences and, as such, do not consider the synchronous effects of multiple habitat use on selection.

Table 5.8: Ranks of habitat types derived from t statistics of averaged log-ratio differences between used and available habitat. + represents relatively more preferred, +++ represents significantly relatively more preferred (P<0.05), - represents relatively less preferred, --- represents significantly relatively less preferred. Higher ranks indicate greater preference.

Spatial scale	Temporal scale	Numerator habitat type	Denominator habitat type			Rank
			1	2	3	
Second order	3&5	1	.	-	-	0
		2	+	.	+	2
		3	+	-	.	1
	7&9	1	.	-	-	0
		2	+	.	+	2
		3	+	-	.	1
	11&1	1	.	-	+	1
		2	+	.	+	2
		3	-	-	.	0
	Annual	1	.	-	-	0
		2	+	.	+	2
		3	+	-	.	1
Third order	3&5	1	.	+	-	1
		2	-	.	---	0
		3	+	+++	.	2
	7&9	1	.	-	---	0
		2	+	.	-	1
		3	+++	+	.	2
	11&1	1	.	+	-	1
		2	-	.	-	0
		3	+	+	.	2
	Annual	1	.	-	---	0
		2	+	.	---	1
		3	+++	+++	.	2

5.3.3 Modelling

Many regression variables were found to be significantly related to utilisation of cells by possums. Models consisted of one to twelve variables, with a mode of three[4]. No significant difference was detected between the mean number of significant variables included in second and third order selection models. Failure to derive a significant model occurred only once (Table 5.9). On average, individual models explained approximately 50 % of the variability in cell use. Some individual models explained nearly all of the variation (e.g. possum 22, third order, 11&1), yet others explained very little (e.g. possum 28, second order, 7&9). Pooled models generally explained less variation than individual based models.

Table 5.9: r^2 values for models derived for individual possums and for pooled data. Second and third order selection represent the spatial scales and the temporal scales are represented by the combined months and the annual data set.

Possum	Spatiotemporal scale							
	Second order				Third order			
	3&5	7&9	11&1	Ann	3&5	7&9	11&1	Ann
14	0.61			0.61	0.67			0.46
20	0.39	0.58		0.53	0.54	0.89		0.38
22	0.84	0.48	0.47	0.83	0.69	0.26	0.95	0.40
24	0.16	0.66	0.28	0.15	0.59	0.33	0.63	0.36
28	0.09	0.10	0.25	0.17	0.81	0.70	0.74	0.43
30	0.63	0.56		0.68	0.37	0.73		0.63
34	0.16	0.34	0.54	0.31	0.89	0.68	0.71	0.23
36	0.17	0.49	0.49	0.29	0.42	0.51	0.31	0.17
42	0.67	0.52		0.57	0.15	0.22		0.12
44	0.62	0.36	0.71	0.83	0.33	0.62	0.91	0.67
46	ns*	0.25	0.29	0.46	0.53	0.18	0.35	0.10
48	0.69	0.60	0.73	0.75	0.65	0.63	0.17	0.62
Mean	0.46	0.45	0.47	0.51	0.55	0.52	0.60	0.38
StdErr	0.08	0.05	0.07	0.07	0.06	0.07	0.10	0.06
Pooled	0.04	0.08	0.15	0.22	N/A			

*not significant

[4] All models are described in Appendix 5.

In general, models included a wide range of variables with no one variable occurring very consistently. Many of the variables deemed significant within models were contradictory between models with respect to the direction of the relationship. Positively related variables occurred more frequently than negatively related ones in models at the second order selection scale (mean difference per model 1.4 ± 0.2); whereas they were approximately equal at the third order selection scale (mean difference per model -0.2 ± 0.3). This difference between the scales was highly significant (F value = 17.6, P value < 0.0001).

Modelling at the second order selection scale indicated that the log-transformed abundance of the top ten preferred species calculated with the annual data set had the most consistent relationship with cell use (Table 5.10). This variable was always positively related to cell use, as was the second most consistent variable, *Pseudowintera colorata* importance value. Modelling at the third order selection scale failed to identify a most consistently occurring variable, as many variables were identified in four or five models (Table 5.11).

Modelling of pooled possum use resulted in only two variables being selected more than once (Table 5.12). These were the log-transformed abundance of the top ten preferred species calculated with the annual data set and *Quintinia acutifolia* importance value. However, *Q. acutifolia* importance value occurred once positively and once negatively, whereas the log-transformed abundance of the top ten preferred species calculated with the annual data set occurred only positively.

It was uncommon for model variables to be exclusively and repeatedly selected in certain seasons, yet *Carpodetus serratus* importance value was selected in a third of the individual models for March/May only at the third order scale. Similarly, *Blechnum discolor* importance value and *Cyathea smithii* importance value were each selected in a quarter of the individual models at the second order scale for March/May only and July/September only, respectively.

Given the inconsistency in selection of variables, derivation of further inferences from the data would be tenuous.

Table 5.10: Frequency of occurrence for variables within models following logistic regression at the second order selection scale for individual possums. Temporal scale is represented by the combined months and the annual data set. Twelve models were derived for the annual data set, 11 for March/May and July/September, and eight for November/January. Frequency was apportioned by whether the variable coefficient was positive or negative. Total frequencies across temporal scales are given as is the total number of times a variable was included in models and the difference between the number of times it was selected as positive and as negative.

Independent regression variable	Frequency											
	Positive				Negative				+ ve	- ve	Total	Difference
	Ann	3/5	7/9	11/1	Ann	3/5	7/9	11/1				
LnPrefOverall	3	3	1	3					10	0	10	10
PSECOL	3	1	2	2					8	0	8	8
CARSER	1	2	3	1			1		7	1	8	6
NERVIL	2	1	1	1					5	0	5	5
RAUSIM	2	1	1	1					5	0	5	5
Ferns	3	1		1					5	0	5	5
BLEFLU	2	2							4	0	4	4
SDI					1		2	1	0	4	4	-4
Tier3					2	1		1	0	4	4	-4
AGRCAP	1	1	1						3	0	3	3
BLEDIS		3							3	0	3	3
CYASMI			3						3	0	3	3
FUCEXC			2	1					3	0	3	3
QUIACU	1		1	1					3	0	3	3
MYRDIV		1		1	3		2		2	5	7	-3
NOTMEN	1	1	2		2				4	2	6	2
RAUANO	1	1	1				1		3	1	4	2
ARISER	1			1					2	0	2	2
ASPBUL	1	1							2	0	2	2
BLEVUL	1	1							2	0	2	2
CYACOL	1		1						2	0	2	2
GRILIT			1	1					2	0	2	2
NERDEP	1	1							2	0	2	2
LnPrefAPR	1	1							2	0	2	2
COPPAR					1	1			0	2	2	-2
TierTOT					1	1			0	2	2	-2
Shrub	1	1		2	1	1		1	4	3	7	1
ASTFRA			1	1	1				2	1	3	1
NEOPED			1	1				1	2	1	3	1
COPROT		1							1	0	1	1
LEPSUP			1						1	0	1	1
LnPrefCondit			1						1	0	1	1
BLEPRO					1				0	1	1	-1
MICAVE							1		0	1	1	-1
PSECON					1				0	1	1	-1
Tier1					1				0	1	1	-1
Tier4								1	0	1	1	-1
SR	1		1		1		1		2	2	4	0
WEIRAC			1			1			1	1	2	0

Table 5.11: Frequency of occurrence for variables within models following multiple regression at the third order selection scale for individual possums. Temporal scale is represented by the combined months and the annual data set. Twelve models were derived for March/May and the annual data set, 11 for July/September, and eight for November/January. Frequency was apportioned by whether the variable coefficient was positive or negative. Total frequencies across temporal scales are given as is the total number of times a variable was included in models and the difference between the number of times it was selected as positive and as negative.

Independent regression variable	Frequency											
	Positive				Negative				+ Sum	- Sum	Total	Difference
	Ann	3/5	7/9	11/1	Ann	3/5	7/9	11/1				
COPRHA		1	3	2	1				6	1	7	5
NEOPED	1				3	2		1	1	6	7	-5
NOTMEN	1		1	3					5	0	5	5
NOTFUS		1			1	2	2		1	5	6	-4
Tier2				1	2	1	1	1	1	5	6	-4
CARSER		4							4	0	4	4
Tier4					1	1	1	1	0	4	4	-4
SR	1	1	2			1			4	1	5	3
PSECRA	1		1	1					3	0	3	3
WEIRAC	1		1	1					3	0	3	3
QUIACU				2	1		1	2	2	4	6	-2
CYASMI				1		1	2		1	3	4	-2
METUMB				1	1	2			1	3	4	-2
BLEVUL					1		1		0	2	2	-2
HOLLAN					1		1		0	2	2	-2
PSECOL		1	1						2	0	2	2
RAUANO					1	1			0	2	2	-2
COPFOE	1		2			1		1	3	2	5	1
ASTFRA	1		1				1		2	1	3	1
BLECOL				1		1		1	1	2	3	-1
COPPAR		1	1				1		2	1	3	1
CYACOL			1			2			1	2	3	-1
TierTOT		2			1				2	1	3	1
BLENOV					1				0	1	1	-1
COPPRO					1				0	1	1	-1
COPROT						1			0	1	1	-1
DICSQU							1		0	1	1	-1
ELAHOO								1	0	1	1	-1
GRILIT						1			0	1	1	-1
HYPRUF						1			0	1	1	-1
MUEAUS		1							1	0	1	1
NERDEP						1			0	1	1	-1
PNEPEN						1			0	1	1	-1
POLVES			1						1	0	1	1
PRUFER								1	0	1	1	-1
PSECON		1							1	0	1	1
RAUSIM								1	0	1	1	-1
SCHDIG				1					1	0	1	1
UNCSPP								1	0	1	1	-1
URTINC		1							1	0	1	1
BLEPRO		1	1	1	1	2			3	3	6	0
BLEFLU		1	1			1	1		2	2	4	0
NERVIL	1		1			1		1	2	2	4	0
AGRCAP		1				1			1	1	2	0
BLEDIS	1							1	1	1	2	0
FUCEXC				1		1			1	1	2	0
LEPSUP		1					1		1	1	2	0
MYRDIV			1					1	1	1	2	0
COVER		1			1				1	1	2	0

Table 5.12: Frequency of occurrence for variables within models following multiple regression for pooled possum use. Temporal scale is represented by the combined months and the annual data set. One model was derived for each scale. Frequency was apportioned by whether the variable coefficient was positive or negative. Total frequencies across temporal scales are given as is the total number of times a variable was included in models and the difference between the number of times it was selected as positive and as negative.

Independent regression variable	Frequency											
	Positive				Negative				+ Sum	- Sum	Total	Difference
	Ann	3/5	7/9	11/1	Ann	3/5	7/9	11/1				
LnPrefOverall		1		1					2	0	2	2
COPRHA			1						1	0	1	1
NERVIL				1					1	0	1	1
PRUVUL				1					1	0	1	1
SCHDIG			1						1	0	1	1
SR	1								1	0	1	1
Herb/Grass				1					1	0	1	1
COPROT					1				0	1	1	-1
ELAHOO								1	0	1	1	-1
NEOPED						1			0	1	1	-1
NOTFUS					1				0	1	1	-1
PSECRA							1		0	1	1	-1
PrefAUG							1		0	1	1	-1
QUIACU			1		1				1	1	2	0

5.4 Discussion

5.4.1 Diet selection

Results obtained from this study agree with those obtained from the study site four years earlier. Although only 36 % of all identified food items were shared between the studies, all of the top ten species identified between January 1998 and May 1999 (Cochrane *et al.*, 2003), comprising 90 % of overall diet, were consumed in this study and comprised 57 % of the overall diet. However, this discrepancy highlights the importance of vegetation heterogeneity on diet analysis; despite little or no change in vegetation structure and composition between studies, differences existed in both the food items that were consumed and the level of consumption of shared food items. These likely arose due to the differing capture locations of possums and differences in availability of seasonal food types such as flowers and fruit.

Possums within the study site have a simpler diet than possums found in more diverse vegetation types, with 46 food items identified in total; Nugent *et al.* (1997) identified 102 food types from a podocarp/hardwood forest in the central North Island and Coleman *et al.* (1985) identified 101 food types from a mixed hardwood forest in Westland. However, as little as 30 food types have been identified in a *Pinus radiata* plantation (Warburton, 1978) and 33 in a south Westland *Nothofagus menziesii* forest (Owen and Norton, 1995). Previous diet work at the study site confirmed the diet complexity with 49 food types being identified on that occasion (Cochrane *et al.*, 2003). The relatively low number of food types consumed in *Pinus radiata* plantations and *Nothofagus* forest may be a reflection of the relatively low diversity of these vegetation types; the suite of potential food types is fewer.

The average number of food types consumed per individual observed in this study (3.3) is generally similar to that observed at other locations in New Zealand; 2.4 - 3.0 (Gilmore, 1967), 4.3 (Sweetapple and Nugent, 1998), 4.9 (Cochrane *et al.*, 2003). But considerably less than that observed in a study in Tasmania that identified 8-12 food types per stomach (Statham, 1984). Nevertheless, it is likely that the number of food items found in possum stomachs is heavily dependent on whether foraging occurred on the ground or in the canopy, as ground feeding is more likely to lead to consumption of multiple food types in the same feeding bout (Sweetapple and Nugent, 1998).

Despite the apparent overall consistency with other New Zealand studies, the number of food types consumed per individual observed in this study did show some significant variation between seasons. The least number of food types was consumed by individuals during winter and was significantly less than the number consumed during summer. This observation may be a reflection of the same process determining the total number of food types consumed by possums within a vegetation type; food is less available during winter when compared to summer. However, many studies have shown no obvious difference in the number of foods consumed between winter and summer (Gilmore, 1967; Warburton, 1978; Fitzgerald and Wardle, 1979; Statham, 1984; Coleman *et al.*, 1985; Owen and Norton, 1995; Cochrane *et al.*, 2003). As such, the few species eaten in winter may be a reflection of possums targeting

widely distributed food items at this time, which would lead to greater overlap in consumption between individuals.

Congruent with other studies, possums in the study site comprised the bulk of their diet with a few staple food items, but also consumed numerous other food items in small quantities. Similarly, considerable variation was observed in the identity of staple food types amongst seasons, which has been postulated to relate to possums' ability to alter their diet in relation to the availability of food items (Harvie, 1973; Fitzgerald, 1976; Fitzgerald, 1978; Warburton, 1978; Coleman *et al.*, 1985; Cowan and Moeed, 1987; Cowan, 1990b; Owen and Norton, 1995; Allen *et al.*, 1997; Cochrane *et al.*, 2003). This behaviour suggests that the minimal consumption of a wide range of food items in addition to staple food items may be a strategy intended to identify potentially beneficial feeding opportunities; if possums were focused solely on obtaining staple food items, such as the strategy of koalas (Cork, 1996; Moore and Foley, 2000), many opportunities to improve diet would be missed.

Possums make extensive use of *Nothofagus* foliage in Tasmania, Australia (Fitzgerald, 1984), yet this study confirms observations made in many New Zealand *Nothofagus* forests that *Nothofagus* foliage comprises an insignificant proportion of possum diet despite being overwhelmingly abundant (Owen and Norton, 1995; Sellar, 1998; Cochrane and Norton, 2000; Cochrane *et al.*, 2003). However, *Nothofagus* foliage consumption of up to 35 % of annual diet has been observed during non-mast years in a *Nothofagus* forest with low abundance of typical possum-preferred species (Sweetapple, 2003). Such a high level of consumption indicates that New Zealand *Nothofagus* species are indeed palatable (Sweetapple, 2003), but are only significantly consumed in the general absence of typical possum-preferred species.

Although there was considerable variation in diet, *Weinmannia racemosa* was clearly the most consistently consumed staple food species. Maximal foliage consumption of this species occurred in winter and low consumption of foliage in summer was compensated by significant consumption of flowers, which is congruent with observations made by Cochrane *et al.* (2003) in the same study site four years earlier. The importance of *W. racemosa* to possums in the study site is logical given its importance in diet in other forests (Gilmore, 1967; Fitzgerald, 1976; Fitzgerald, 1978;

Fitzgerald and Wardle, 1979; Coleman *et al.*, 1985; Allen *et al.*, 1997; Nugent *et al.*, 1997; Cochrane *et al.*, 2003) and its extensive distribution (Chapter 4). It is likely that this species plays a key role in determining possum density because possums' reliance on it is highest during winter when possums are at most risk to starvation-induced mortality (Brockie, 1992).

Preferences for plant species varied markedly between the seasons. Only five food types occurred as one of the top ten preferred food types in more than one season. Curiously, the only one that did so in all seasons was *Neomyrtus pedunculata* foliage, a species commonly recognised as being unimportant in possum diet (Nugent *et al.*, 1997; Cochrane *et al.*, 2003). Of the others, *Rubus cissoides* foliage was highly preferred in April and August, *Weinmannina racemosa* foliage was moderately preferred in April and highly preferred in August, *Nertera depressa* foliage was moderately preferred in August and December, and *Ranunculus repens* foliage was lowly preferred in August and December. There is support for the high preference for *Rubus cissoides* with one study indicating that it is a preferred species (Owen and Norton, 1995), yet commonly it is sparsely consumed (Warburton, 1978; Coleman *et al.*, 1985; Cochrane *et al.*, 2003) and is relatively unpreferred (Nugent *et al.*, 1997; Cochrane and Norton, 2000). However, it must be recognised that being sparsely consumed does not predispose a species to low preference and, furthermore, the importance of *Rubus cissoides* is likely to be greatest when there is a lack of generally more preferred species, such as occurs in floristically simple forests (Sweetapple, 2000). The high preference for *Weinamnnia racemosa* indicates that its consumption is not simply a function of its high availability and further highlights the importance of this species to possums. Possums' preference for *Nertera depressa* and *Ranunculus repens* within the study site is somewhat anomalous when compared to other diet studies and may be an artefact of sampling errors associated with infrequently consumed and available species.

Of the most preferred food types identified in each season, *Fuchsia excorticata* foliage (December) and *Muehlenbeckia australis* foliage (April) have been identified as highly preferred in other studies (Owen and Norton, 1995; Nugent *et al.*, 1997). The highest preference for *Carpodetus serratus* fruit in August is not reflected in the literature; however, use of this food type has been observed in other studies (Coleman

et al., 1985; Cowan, 1990b) and given the paucity of other food types during winter possums' high preference for this food type is logical. It is difficult to determine whether seasonal change in preference is a direct response to the perceived decrease in profitability of a food type or the perceived increase in profitability of others, although it is likely to be a function of both.

Overall preference ranking indicated that *Fuchsia excorticata* foliage was the most preferred plant food type in the study site, with *Carpodetus serratus* fruit second and *Rubus cissoides* foliage third. However, when average preference was calculated for only those possums that consumed a particular food type, *Carpodetus serratus* fruit was considered the most preferred with *Pseudopanax colensoi* fruit second and *Aristotelia serrata* fruit and flowers third. Under this method of calculation, food types that are consumed infrequently but abundantly are well represented, which applies especially to those food types that are unavailable seasonally. When diet preferences are simply averaged across individuals and seasons the bias is towards frequently consumed food types, which are likely so as a result of extensive distribution. It is likely that fruit and flowers are more difficult for possums to locate than foliage, which explains why their frequency of consumption is lower. However, it appears that once these food types are located they are highly consumed, suggesting that they are a highly desirable resource. This contention is supported by the observation that fruit consumption is correlated with availability (Gilmore, 1967; Coleman *et al.*, 1985; Cowan, 1990b; Nugent *et al.*, 1997); such a pattern of consumption suggests that possums select fruit ahead of other food types on the merits of fruit rather than decreasing availability of other food types, because fruit is eaten regardless of the time of the year in which it becomes available (Cowan, 1990b).

High protein foods such as fungi and invertebrates were highly consumed within the study site (25 % when fungi and invertebrates are combined with co-consumed litter and wood), with fungi in particular forming a very large component of overall diet (16 % when co-consumed litter and wood included). This consumption level is considerably higher than that observed in other studies and may reflect a foliar protein deficiency within the staple food species, *Weinmannia racemosa* (Fitzgerald, 1976). However, there is evidence to suggest that much of the protein contained by some fungi is unavailable to mammals (Claridge and May, 1994). This suggests an

alternative explanation; high consumption may simply reflect high availability during the diet study. Additionally, the consumption of fungi may have been influenced by the lack of other highly preferred food types present at more diverse sites (e.g. Sweetapple, 2003). Nevertheless, opportunistic (use of ephemeral resources) feeding has been observed on fungi (Gilmore, 1967; Statham, 1984; Claridge and May, 1994; How and Hillcox, 2000; Cochrane *et al.*, 2003; Sweetapple, 2003) and invertebrates (Warburton, 1978; Cowan and Moeed, 1987; Owen and Norton, 1995) in other areas. The decision to switch to consumption of fungi and invertebrates when available implies high preference for these food types, as they are generally less available than foliar food types.

Although significant use of *Nothofagus* seed has been detected in other studies (Sweetapple, 2003), no evidence of this was detected in this study, likely because the diet sample was not taken in a mast seeding year. This food type can be very important to possums in otherwise low quality forest and can greatly increase population levels following mast years (P. Sweetapple pers. comm.).

Often seasonality of diet is reported in studies, yet most inferences are drawn from the average importance of food types. As such, much of the variability within this data is masked. Consider the case where within each season a different suite of staple food types is consumed yet additional species are consumed consistently but in small quantities. When these data are averaged for all seasons the situation may be encountered whereby all food types are shown to be consumed equally. In this case it could be concluded that a food type that was consumed in large quantities in one season, but not consumed in others is as important to possums as a food type that is consumed in small quantities throughout all seasons. However, the seasonally important food type may be absolutely essential to winter survival and the ability to raise offspring (Williams, 1982), whereas the more consistently consumed food type may be forgone without serious consequences for reproduction and survival. As such, in this study, it could be argued that *Carpodetus serratus* fruit should be considered more important to possum diet than *Neomyrtus pedunculata* foliage, despite its overall level of use being less, because it is a very important constituent of winter diet whereas *N. pedunculata* foliage is consumed throughout the year in smaller quantities.

The definition of what constitutes a food type is somewhat unclear in the literature, especially in the case of material that appears to have been ingested incidentally whilst another food type is being targeted. In this study, consumption of fungi and invertebrates was frequently associated with consumption of leaf litter and rotting wood, as these items were observed together within stomach layers. It is logical to assume that the intention of possums was to obtain either fungi or invertebrates, yet the decision to also consume wood and leaf litter is a significant one. If we assume that possums prescribe to optimal diet theory, then decisions to consume particular items are parameterised by the products of their costs and benefits (MacArthur and Pianka, 1966; Newman *et al.*, 1995; Cork, 1996; Hanley, 1997; Hirakawa, 1997). Furthermore, diet selection is constrained by digestion (Hirakawa, 1997), so the opportunity cost of deciding to not consume alternative food items must also be considered (Lucas, 1983). Put in this context it becomes apparent that the consumption of large amounts of litter and wood cannot be disregarded when the relative merits of food types are considered. If we assume that the nutritional benefits of litter and wood consumption are minimal, then their consumption represents a cost that is offset by the benefits attributable to the consumed fungi or invertebrates; this suggests that the value of fungi and invertebrates is proportional to the total mass of items within the stomach layer in which they occur, not just their individual mass. As such, fungi and invertebrates are likely to be important possum diet constituents in *Nothofagus* forest, although assessment of their availability would be necessary to elucidate preference for them.

Possums have frequently been described as opportunistic feeders (Warburton, 1978; Cowan and Moeed, 1987; Brown *et al.*, 1993; Cochrane *et al.*, 2003) and this study further strengthens that contention with approximately 50 % of the diet attributable to ephemerally available food types. This unusually high abundance of non-foliar food types is likely a reflection of the low diversity of *Nothofagus* forest and the relative lack of highly preferred species (Sweetapple, 2000). As such, possums are likely augmenting their relatively poor foliage diet with seasonally abundant and potentially high-energy resources (Williams, 1982; Claridge and May, 1994).

Evidence for the dependency between the various scales of resource selection can be seen in the significant negative relationship between home range size and forage

quality. A large part of possum foraging is likely attributable to diet selection. Forage quality affects how easily a possum can obtain an adequate diet and hence poorer quality in forage requires greater distances to be travelled for this diet to be obtained, as is predicted by the food exploitation hypothesis (Larter and Gates, 1994). Biases in these movements are likely to arise as possums attempt to maximise energy (Belovsky, 1986b) by foraging in more productive areas, which is a process that proceeds at the scale of habitat selection.

5.4.2 Habitat selection

Possums chose the location of their home range within the study site randomly, with respect to the defined habitat types. Analysis at the second order selection scale indicated that there was only a 25 % chance that non-random selection was occurring, regarding the annual data set. Similar to the second order selection scale, possums exhibited no significant overall selection between habitat types at the third order selection scale, although overall non-random habitat use was approached at the March/May and annual temporal scale. From the calculated P values we can say that there was a 91 and 94 % chance that overall non-random habitat use was occurring at these scales, respectively. When the pairwise differences in use between habitat types are examined it becomes apparent that habitat type three was the only one that was significantly more preferred than any of the others; at the March/May temporal scale it was significantly more preferred than habitat type two, at the July/September temporal scale it was significantly more preferred than habitat type one and at the annual temporal scale it was significantly more preferred than both.

These results are somewhat curious considering most of the highly preferred species are located within habitat types one and two. However, it must be recognised that preference for food items is independent of the amount of time spent feeding on them, whereas preference for habitat is dependent on residence time. Thus inferences for habitat selection based purely on the presence of preferred species are somewhat misguided. When moving between these scales it is most useful to consider percentage composition of diet instead of relative preference because possums likely spend most foraging time feeding on staple food items. In this case we would expect habitat type two to be most highly preferred as it contains by far the greatest

abundance of the most staple food type, *W. racemosa*. However, the distribution and abundance of fungi and invertebrate may provide a confounding influence, as these food types were ranked second and third by percentage consumption, respectively. Although this was not formally assessed, the interpolated surfaces of their distribution in possum diet shows that stomachs containing high proportions of fungi and invertebrates most commonly came from possums caught in habitat type three. However, this does not prove that these food types were consumed there, only that the likelihood of them being consumed there is greater than for the other habitat types. Similarly, the consumption of *Rubus cissoidies* in habitat type three is also implied. Although tenuous, this evidence suggests that there may be more nutritional value in habitat type three than expected. It must be recognised though that non-diet related factors may also have influenced this pattern of selection.

Nevertheless, overall tests of selection indicated that possums were not significantly discriminating between habitat types. There are six possible scenarios or factors that may explain the failure to detect significant overall selection: non-feeding behaviour; sensitivity to resource levels; fine-scale selection; distinctiveness of habitat boundaries; spatial pattern of habitat types; and bias. These are outlined as follows:

1) The premise that possums, as generalist herbivores, are likely energy/nutrient maximisers and emphasise the importance of foraging (Belovsky, 1986a) suggests that non-feeding behaviour should have less influence on habitat selection than foraging. However, this may not be the case with possums in the study site. When it is considered that feeding behaviour constitutes approximately 10-20 % of overall activity (MacLennan, 1984), it seems logical to assume that 80-90 % of the time possums are responding to stimuli other than appetite. The low overall utilisation of apparently high quality habitat types suggests that these non-appetite stimuli negate utilisation of these areas. In addition, it is entirely plausible that feeding behaviour may actually conflict with the satisfaction of these stimuli. In some cases this trade-off effect may remove the correlation between habitat selection and food availability (Mysterud *et al.*, 1999). For example, predation, in the form of spotlight hunting, was undoubtedly the greatest at the roadside and it is likely that this resulted in a degree of wariness in possums living near this area (B. Warburton

pers. comm.); as such, the effective availability of roadside areas would have been decreased (Mysterud and Ims, 1998). However, McDonald-Madden *et al.* (2000) failed to observe a trade-off between foraging and predation for the brushtail possum in an urban setting in Australia. Furthermore, possums spend most time sitting still or grooming, which are activities that typically follow feeding (MacLennan, 1984). Correlation between these behaviours and feeding should be expected, although it must be recognised that predation risk may modify this correlation.

2) When resources are considered we commonly make the assumption that more is better, but do threshold densities exist above which an individual possum does not discriminate? Studies have indicated that in areas of highly abundant food animals may exhibit selection on the basis of preferred species presence rather than biomass (Marell *et al.*, 2002). At population densities below carrying capacity there is likely to be abundant food for all individuals and therefore individual health is not likely to be limited by available food. Under this scenario possums are unlikely to be highly discriminatory as many areas are likely to be equally profitable or adequate for fitness; there is no explicit advantage for selecting areas containing highest abundance of resources. However, as population levels rise, food availability would become a limiting factor and the number of areas above the threshold food density would decrease to zero. Discrimination between areas would likely follow because doing so would have major benefits to individual fitness (MacArthur and Pianka, 1966). Because possum densities were well below carrying capacity during the study (M. Bygate pers. comm.) food availability would not have been a limiting factor on individual fitness and discriminatory behaviour would have been minimal.

3) Often animals are assumed to make preferential use of the best habitat available to them (Hanski, 1989), but habitat quality is determined by the distribution of resources and is thusly dependent on the scale at which it is observed (Southwood, 1977; Wiens, 1989b; Kotliar and Wiens, 1990). It has been suggested that this scale is finer for smaller animals (Norbury and Sanson, 1992), inferring that small animals have the ability to exploit small high quality patches. Possums, as small generalist herbivores, select at the tree or tree

cluster scale (Jolly, 1976; Meads, 1976; Ward, 1978; Payton, 2000). Consistent use of individual trees has been observed (Meads, 1976) and may represent a strategy to improve the nutritional properties of browse (Payton, 2000). Therefore, possums may not perceive a value difference between a tree alone and a tree amongst others of the same species. As an extension, different habitat types could have significantly different value at the broadest scale yet have the same value at the finest scale.

4) The distinctiveness of habitat boundaries and the internal homogeneity of habitat types, with respect to classification parameters, are of utmost importance for habitat selection analysis because the tenet underlying this process is optimal use of a *patchy* environment (MacArthur and Pianka, 1966). The standard definition of a habitat type or a patch is that of a spatially discrete and internally homogeneous unit (Kotliar and Wiens, 1990). However, this definition is critically dependent on the spatiotemporal scale of observation (Wiens, 1989b; Kotliar and Wiens, 1990; Levin, 1992; Wiens *et al.*, 1993). The ability to distinguish between habitat types should be deemed a prerequisite for selection between them.

Following classification of the vegetation in the study area, many constructed boundaries between habitat types did not follow obvious floristic discontinuities. Boundaries between habitat types would have been most recognisable to possums as gradual transitions from one habitat type to the next, as opposed to abrupt discontinuities. Consequently, behavioural responses to these boundaries are likely to have been minimal (Kolasa and Rollo, 1991). This problem of habitat type boundary intangibility is essentially attributable to the low overall heterogeneity within the study site. In more heterogeneous landscapes, boundaries between habitat types such as forest and grassland are abrupt and environmentally distinct, and lend themselves to distinguishability (Hansen and di Castri, 1992; Fortin and Drapeau, 1995). Essentially this is a shortcoming of the use of 'patches' as the selection unit, when in fact 'patches', in their true sense, are rare in nature (Kotliar and Wiens, 1990).

Problems regarding detection of consistent habitat selection in areas of low habitat heterogeneity have been reported in the literature. For example, Aberg *et al.* (2000) failed to detect consistent patterns of habitat selection in hazel grouse throughout a predominately coniferous forest in south-central Sweden. This was despite analysis at multiple scales, using two habitat descriptions, a 10 year data set and a detailed vegetation description. They postulated that their inability to detect consistent selection patterns was attributable to the general suitability of most habitats within the study area, and that probability of detecting selection would likely increase with increasing variation between habitats.

5) A frequently overlooked and potentially confounding aspect of habitat selection analysis is that of spatial pattern of habitat types (Porter and Church, 1987; Otis, 1998; Wilson *et al.*, 1998). Attributes of spatial pattern dictate the likelihood of interception and persistence by animals (Forman and Godron, 1986; Gutzwiller and Anderson, 1992), the sensitivity of habitat selection analysis to habitat availability estimations (Porter and Church, 1987) and the level of correlation between the utilisation of neighbouring habitat types (Otis, 1998). Although the components of spatial pattern can be measured using complex landscape metrics such as contagion, juxtaposition, interspersion and fractal dimension, they are difficult to integrate with habitat selection models (Otis, 1998) and require distinct habitat units. Nevertheless, less complex components of spatial pattern such as patch size and shape may still hold valid inferences for habitat selection in this study. The likelihood of an animal encountering a habitat type is influenced by the shape and spatial orientation of that habitat type. If a habitat type is relatively linear and aligned perpendicular to the direction of animal movement, then the likelihood of animal encounter is high (Forman and Godron, 1986; Gutzwiller and Anderson, 1992). Conversely, if a relatively linear habitat type is aligned parallel to the direction of movement, then the likelihood of animal encounter is low (Forman and Godron, 1986). It follows that a rounded habitat type of similar area would have an intermediate likelihood of animal encounter.

In the context of this study, these scenarios suggest that the linearly aligned habitat type one would have had a high probability of encounter in relation to its small size, as too would the section of habitat type two on the escarpment. Despite this and the fact that many preferred plant species are located within these vegetation types, no significant preference was observed for them. This behaviour could be partially explained by the shape properties of these vegetation types; both have a high ratio of edge to interior and, consequently, the likelihood of possum persistence is low (Forman and Godron, 1986). It is highly likely that the attractiveness of the habitat types containing abundant preferred species is proportional to the appetite of individual possums. It follows that once a possum becomes satiated as a result of feeding in such habitat types its likelihood of persistence is minimal, as even small random movements are likely to involve the crossing of boundaries with other habitat types. Consequently, the utilisation of neighbouring habitat types will be inflated. In which case, the use of habitat types adjacent to habitat types containing abundant preferred species is possibly driven by the merits of their neighbour rather than by merits of their own.

6) Although the successful detection of selection appears to be primarily limited by the environment, experimental bias also influences the outcomes of habitat selection analysis. Bias is introduced in any study of habitat selection by many factors such as the errors associated with radio telemetry (Rettie and McLoughlin, 1999), the scale of habitat classifications (Wiens, 1989b), and the estimation of habitat availability (McClean *et al.*, 1998). This study was no exception. Bias was likely present at all scales examined and, in particular, analysis at the second order selection scale must be considered with a degree of uncertainty. It is likely that these analyses were biased not only by the definition of availability (Johnson, 1980; Warnock and Takekawa, 1995; Arthur *et al.*, 1996; McClean *et al.*, 1998), but also by the sampling of individuals within the population. Although the definition of availability at the second order scale did attempt to take into account biological parameters such as reluctance to cross major waterways and the potential of movement, a better definition would perhaps take into account the dispersal potential of juvenile possums, as it is likely that possums select their future home ranges at this stage

of development (Cowan, 2000b). However, this approach would require a long-term study following possums from juvenile dispersal through to adult stability, supported by a detailed description of habitat availability over a large area and perhaps an assessment of the densities of conspecifics throughout. This bias attributable to the definition of availability at the second order selection scale is potentially quite large due to the aggregated nature of habitat types in the study site (Porter and Church, 1987).

The second source of bias at the second order selection scale was likely introduced by the possum sampling procedure. Sampling effort was not allocated to habitats in proportion to their area; rather, it was focused towards roadside and streamside areas. Consequently, the use of the wider study area as the definition of availability does not accurately match the distribution of the study possums. To avoid this bias a more random sampling strategy would have been desirable. Nevertheless, a random sampling approach would have been very difficult to implement because of the time lag between captures and the necessity to radio collar each possum as quickly as possible; random sampling would have required a random sample of animals to be caught concurrently, from which a further random subsample would have determined which animals would carry radio-transmitters. This approach would have required an extensive trapping grid and numerous field assistants in continuous radio contact with a sampling co-ordinator. The financial costs of this approach rendered it inappropriate for this study.

Unlike the second order selection scale, habitat selection at the third order scale is reasonably independent of the sampling regime chosen. Nevertheless, a robust and representative sample of animals is still required if population inferences are to be made. Fortunately, the studied sample of possums, although small, was a good representation of the overall population, due to the even distribution of sex and age. Another advantage of the third order scale is that bias associated with availability estimation is significantly decreased as a result of individual assessment. Consequently, inferences made at the third order selection scale can be stated with reasonable confidence.

In conclusion, it is possible that all, some, one or none of these explanations hold sway within the study site, but it seems likely that the inability to detect clear habitat preferences is primarily attributable to the characteristics of the site rather than the lack of selectivity by possums in a general sense.

Ultimately, habitat selection analysis has the ability to assess the suitability for stratification of possum management operations such as control and monitoring. Doing so has the potential to improve overall precision and economy of management operations on both regional and local scales (McCallum, 2000). However, habitat selection analysis proceeds at multiple scales and the implications of the scales for stratification vary; although second order selection may indicate preferred home range location, third order selection determines the distribution of activity through different seasons. The fact that a habitat type is preferred at the second order scale does not necessarily indicate that activity will be high in it (Orians and Wittenberger, 1991) and, therefore, failure to consider multiple scales can be detrimental to effective stratification. If general insights into possum density are required then the second order selection scale likely holds the most inferences. Such information might be useful for the management of bovine tuberculosis in indigenous landscapes, as the viability of this disease in possum populations is dependent on possum density (Barlow, 1991b; Barlow, 1991a; Caley *et al.*, 1998). However, if areas of high local activity are of more interest then analysis at the third order selection scale will provide the most pertinent information. Such information may prove beneficial in the study of interactions between possums and monitoring devices, which has been identified as an important consideration when dealing with low population densities (B. Warburton pers. comm.). This scale may also provide useful information for the timing of control and monitoring operations as it elucidates temporal variability.

Because clear preferences for habitat types were not identified in this study, stratification should be considered infeasible within the study site; as such, it should be treated as a single management unit, not three separate habitat types. This outcome could be viewed in two complementary ways: first, as a failure to detect significant patterns of space use by possums and, second, as a successful assessment of the suitability of study site stratification.

5.4.3 Modelling

On average, models exhibited low r-square values (individual models 0.38 - 0.60, pooled models 0.04 - 0.22) which rendered them unsuitable for predictive purposes. Nevertheless, they still hold inferences for the relationships between possums' use of space and resource distribution in an exploratory sense (Morrison *et al.*, 1992).

It is interesting to note that models derived at the second order selection scale were significantly more likely to include positively related variables, yet models derived at the third order scale showed no such bias. This may hold insights into the processes involved for selection at the second order scale. It would seem that possums were selecting the location of their home ranges on the basis of preference, not avoidance. Put another way; possums will tolerate the presence of unpreferred resources provided preferred resources are present.

The relationships between resource variables and possum use cannot be viewed as cause and effect, as we have no way of knowing whether possums used certain areas as a result of obtaining a resource or if use was simply correlated with the presence of that resource. Confusion may arise when correlations occur through chance, although the repeated presence of a correlation for different individuals would indicate that it is, in fact, genuine.

Despite the fact that nearly all of the models derived represented significant relationships between possum utilisation and resource variables, much variability existed in the inclusion of variables in models between individual possums. Modelling at the second order selection scale indicated that most frequently possums chose their home range in areas with high values of the log-transformed abundance of the top ten preferred species as defined by the annual possum diet data (hereafter termed 'LnPrefOverall'). However, it must be recognised that only ten models out of a possible 43 included this variable. Similarly, the next two most frequent variables, *Pseudowintera colorata* abundance and *Carpodetus serratus* abundance, both positively related to individual possum presence, were only included in eight and six models, respectively. Interestingly, *C. serratus* abundance was most consistently included in models during the July/September period, which corresponds well with

the season in which *C. serratus* fruit was regarded the most preferred and was also consumed in high amounts. Also of interest is the apparent conflict between the LnPrefOverall variable and *C. serratus* abundance. It would appear that these variables are negatively related and may represent a seasonal shift in possum use. Indeed, the distribution of *C. serratus* appears to be negatively correlated to that of the combined species represented by the LnPrefOverall variable.

Although negatively related variables were less frequently included in models, some of them were included multiple times. Shannon diversity index and tier three were both exclusively negatively related to individual possum presence. This would suggest that some possums tended to locate their home range in less diverse areas with lower shrub densities. There may be some degree of positive correlation between these variables because the shrub component contains a large proportion of the species present within this forest. Regardless, none of these variables were consistently selected in models for most or all of the possums studied.

This problem was more pronounced for modelling at the third order selection scale. However, *C. serratus* abundance was exclusively selected in models as a positively related variable for a third of the possums in the March/May season. When it is considered that several of the radio-tracked possums had very sparse *C. serratus* within their home ranges and were consequently unlikely to respond to it, the inclusion of *C. serratus* in a third of the models becomes more significant. Although the fruit of this species was shown to be most highly consumed in August of the year following radio-tracking, it has been observed in other studies to be most commonly consumed in April and May (Cowan, 1990b). This suggests that at least a third of the radio-tracked possums were potentially utilising this resource at this time, although other diet unrelated factors driving the correlation between possum use and *C. serratus* abundance cannot be ruled out.

Pooling of possums for the purposes of modelling introduces biases associated with sampling of the studied possums. However, this bias was reduced by averaging cell use amongst possums and by omitting unused cells from analysis. Given the high variability of variable inclusion in models demonstrated at the second order selection scale, the identification of significant variables using pooled data becomes more

unlikely. As such, the presence of such variables holds greater implications for the possum population within the study site when compared to models derived for individuals. The low r-square values for models derived with the pooled data set reflect the variability encapsulated by pooling individuals. Because of this they have no predictive value, only exploratory value. The only variable that was selected more than once with the same direction of relationship for the pooled data set was LnPrefOverall. This supports the frequent selection of this variable in individual models at the second order selection scale. It appears that possum presence is positively correlated with the species represented by the LnPrefOverall variable. This correlation was not present for the July/September season, which may well have caused it to not be identified for the annual data set also. Intuitively it could be expected that possums were present in areas with high LnPrefOverall values because of their high foraging value; however, the failure to identify the seasonally-specific LnPrefApr, LnPrefAug and LnPrefDec variables in pooled models suggests that this correlation is not purely diet related and likely contains an element of stochastic correlation.

It appears as though the remaining positive correlations with cell variables and possum use of those cells likely represent less direct diet influences, as none of them were explicitly identified as important in possum diet within the study site. *Prunella vulgaris* and *Schefflera digitata* both had limited distributions within the study site and have, therefore, little value as explanatory variables for the pooled data set. Conversely, the herb/grass and species richness (SR) variables were widely distributed. The identification of the herb/grass variable as significant for the November/January season model correlates well with the season in which herbs and grass combined had the greatest importance to possum diet, December. The explanation for the SR variable is less straightforward, although intuitively greater diversity may provide greater feeding opportunities.

Eight negatively correlated variables were identified for the pooled data set, but only three of them had sufficiently broad distributions to provide explanatory value. Curiously, two of these variables had strong links to diet preference; *M. australis* and the summed abundance of the top ten preferred species identified with the August diet sample (hereafter termed 'PrefAug'). Furthermore, the variable PrefAug was only

included in the model derived for the season to which it is most related, July/September. It would seem unlikely that possums avoided cells in direct relation to the properties of the variables within the cells because these very properties have been shown to be selected by possums within diet. This observation more likely arises as a result of a correlation between these variables and other factors not included as potential explanatory variables that decrease the likelihood of cell use, or as a result of biases associated with pooling data across individuals.

The other negatively related variable, *N. fusca*, had the most continuous distribution within the study site and, therefore, provided the best explanatory value. Because this variable was selected for the annual data set, it is inferred that possum activity is highest throughout the year where *N. fusca* abundance is lowest. As *N. fusca* is undoubtedly the most dominant species present, where its abundance is lower other plant species abundance is higher. Given that *N. fusca* is unpreferred, possum foraging would likely be more rewarding in areas of lower *N. fusca* abundance. Viewed in this way, the inclusion of *N. fusca* as a negatively related variable complements the inclusion of LnPrefOverall as a positively correlated variable.

Modelling of possum use data over multiple scales has indicated that there is great variability in the correlations between cell use and cell attributes amongst possums. This may be a reflection of the inherent variability exhibited by brushtail possums (Kerle, 1984), inaccuracy of variable assessment or that the unit of measurement is not congruent with the way possums perceive their environment (Morrison *et al.*, 1992). It is likely, as has been mentioned previously, that possums select resources on a much finer scale than the 0.5 ha cells used to define resource distribution. More intensive models could be developed with very fine scale assessment of possum use and resource distribution, but such models are very limited in their application as they become very site specific (Morrison *et al.*, 1992).

5.4.4 Resource selection

The definition of what resources are available to a forager is one of the most critical components of a resource selection study (Johnson, 1980; Porter and Church, 1987; Warnock and Takekawa, 1995; McClean *et al.*, 1998). Many researchers use the term

as an absolute by restricting it within boundaries either defined arbitrarily or with parameters attributable to the study organism (Thomas and Taylor, 1990). This belies the true complexity of availability: To most accurately represent availability we should include the currency of animal fitness; cost and benefit (Kamil *et al.*, 1987; Bell, 1991). As such, availability can be defined by the parameters outlined in optimal foraging theory. It seems logical to do this because optimal foraging theory is commonly assumed as the mechanism driving resource selection (MacArthur and Pianka, 1966; Rosenzweig, 1985; Stephens and Krebs, 1986; Kamil *et al.*, 1987; Hughes, 1993). Essentially, an optimally foraging animal decides to select a resource if its benefits outweigh its costs (MacArthur and Pianka, 1966; Stephens and Krebs, 1986). Costs terms have been defined as: travel, search and handling time (MacArthur and Pianka, 1966; Stephens and Krebs, 1986; Kamil *et al.*, 1987); digestive constraints (Penry, 1993; Hirakawa, 1997); predation risk (Mysterud and Ims, 1998); opportunity cost (Lucas, 1983); competitive interactions (Sih, 1993); and thermoregulatory expenditure (Schmitz, 1991). These costs can be grouped as internal or external constraints (Bell, 1991), yet they are unified in determining how available a resource is to a forager.

Viewing availability as the cost component of an optimal foraging model facilitates an understanding of resource switching by possums. The generalised optimal foraging theory defines the profitability of a resource as the product of the costs and benefits incurred obtaining it (Stephens and Krebs, 1986; Kamil *et al.*, 1987). Intuitively, we can expect a resource to diminish in profitability with increasing costs associated with obtaining that resource, assuming that their benefit remains constant. If this profitability determines the relative preference of a resource, given a suite of resources, we can define threshold costs at which a resource switches its relative preference rank with the one below it. In the case of possums, this switching behaviour, as opposed to utilisation proportional to availability, is supported by the observation that diet is limited to high consumption of a small number of food types that vary spatiotemporally (Fitzgerald, 1976; Fitzgerald, 1978; Warburton, 1978; Fitzgerald and Wardle, 1979; Fitzgerald, 1984; Owen and Norton, 1995; Cochrane *et al.*, 2003). Optimally foraging possums, as generalists herbivores and likely energy maximisers (Belovsky, 1986b), are expected to consume the most profitable food types almost to the exclusion of food types that could potentially sustain them, but are

less profitable. However, if this relative profitability of food types changes, as a result of changing cost, a switch in the food types that comprise the bulk of the diet is likely to occur. Further, this switch in diet is likely to be accompanied by a switch in habitat utilisation, due to the spatiotemporal heterogeneity of palatable species; a link observed with other animals (Kamil *et al.*, 1987; Turner *et al.*, 1997; Brown, 2000). A critical assumption of this switching theory is that possums have an extensive knowledge of their feeding environment, which is supported by possums' stable home ranges, their tendency to target specific trees or stands within their home range, and their utilisation of seasonal food sources (Crawley, 1973; Jolly, 1976; Meads, 1976; Ward, 1978; MacLennan, 1984; Brockie *et al.*, 1989).

Costs such as travel time and search time can be partially accounted for in a relative sense by defining availability as the proportion of a resource, usually by some index of abundance (Morrison *et al.*, 1992), within a defined area because abundance is assumed to be correlated with these costs. Clearly, this is a gross simplification of true availability and the validity of such an approach hinges on the assumed correlation between abundance and cost. Furthermore, estimations of availability using this approach are likely to contain a large error component attributable to the scale at which it is defined (Johnson, 1980; Porter and Church, 1987; Warnock and Takekawa, 1995; Arthur *et al.*, 1996; McClean *et al.*, 1998).

When resource preference is calculated using these estimations of availability the error component is included implicitly. The effect of variability in the definition of availability on preference analysis outcomes can be appreciable (Warnock and Takekawa, 1995; McClean *et al.*, 1998) and the propriety of such outcomes can be questioned (Johnson, 1980). This contention is supported by the rank preferences obtained for the possum diet preference analysis; there was frequent disagreement between the ranks obtained with the seven different spatial scales used to define availability. Given this observation, the validity of choosing a single arbitrary scale for the definition of preference is questionable, especially in heterogeneous environments.

In New Zealand, diet preference information is commonly used to infer susceptibility of plant species to impacts by introduced herbivores (Forsyth *et al.*, 2002). Given the

error and bias involved in the estimation of diet preference, the validity of inferring susceptibility can only be guaranteed at the finest scale and in general terms. Validity is likely to be compromised when scaling up to infer susceptibility of forests to herbivory because errors are compounded, especially so for species that are highly preferred but patchily distributed.

Resource preference analysis typically compares resource use with its availability (Manly *et al.*, 1993). To continue the benefit versus cost analogy; because availability (cost) is accounted for, resource preference analysis seeks to elucidate the relative benefits attributable to resources. Resource selection then reflects the trade-offs between these benefits and the environment. In this case the question needs to be asked; why do we seek to account for availability with field studies of resource preference? Attempting to do so blurs the lines between field resource selection and cafeteria style experiments where resource availability is controlled by offering equal abundances of resources to captive animals. Perhaps a suitable direction for future research in this area would be examination of the interactions of the different components of availability with the view of building a model to explain the product of their influences. Doing so would shift focus from examination of the explicit properties of resources to the broader question of why resources are selected.

Modelling, as a means for evaluating relationships between animals and resources, avoids many of these problems and may be especially beneficial when resources are not aggregated into distinct patches. This approach is less sensitive to observer bias provided that measurement units are equal to or below the scale at which animals exhibit selectivity because resources need not be classified (Morrison *et al.*, 1992). Modelling also has the useful advantage of potential predictive capability, provided model parameters are robust (Morrison *et al.*, 1992). This predictive capability has the potential to become a useful aid for managing introduced herbivores in New Zealand as it could be used to identify areas with potentially high herbivore density and could also predict herbivores' response to control, such as reinvasion.

5.5 Conclusions

Possums within the study site exhibited diet preferences similar to those observed in other forest types. Foliage, in particular that from *Weinmannia racemosa*, formed the basis of possum diet, yet fruit and flowers were highly preferred, especially when calculations of average preference only included those possums that consumed particular food types (conditional mean). Given also the high consumption of fungi and invertebrates, possums in the study site were probably augmenting their diet with non-foliar food types to compensate for relatively poor forage quality when compared to many other New Zealand forest types (e.g. podocarp/broadleaved forest).

Diet preferences were not clearly reflected by habitat selection analysis, as the most preferred habitat type contained the lowest abundance of preferred species. However, many factors other than abundance of preferred species could have been influential in determining this pattern. Modelling indicated that the use of 0.5 ha cells by possums was frequently significantly correlated with resource variables, yet considerable variation was exhibited in which resource variables were included in models. Nevertheless, preference-based resource variables were the most commonly occurring in models, which indicates that the abundance of preferred species does influence possum movements. This is further supported by the positive relationship observed between home range size and forage quality, as defined by the abundance of preferred species.

These findings and those from the previous two chapters are synthesised within context of each other in the following chapter in order to derive a conceptual model of resource selection by possums within the study site. Management implications and further research questions are also discussed.

Chapter 6: Final conclusions

The purpose of this chapter is to outline some of the major findings from preceding chapters and to then relate them in order to derive a conceptual model of possum resource use within the study site. The findings of this study are then put into context with current management of possums in New Zealand and potential areas of future possum research are proposed.

6.1 Synthesis

Comprehensive studies of possum ecology within New Zealand are scarce. Many studies have investigated diet (*see review* Nugent *et al.*, 2000), several have investigated movements (*see review* Cowan and Clout, 2000), few have investigated both in conjunction (e.g. de Zwart, 2002) and fewer still have sought to relate movement parameters to underlying spatiotemporal variability in vegetation (e.g. Jolly, 1976; de Zwart, 2002). The only forests that have been subject to comprehensive studies of possum diet, movement and population demographics occurred in the Orongorongo Valley, Wellington (see Mason, 1958; Ward, 1972; Crawley, 1973; Fitzgerald, 1976; Meads, 1976; Ward, 1978; Ward, 1984; Ward, 1985; Cowan and Moeed, 1987; Cowan, 1990b; Allen *et al.*, 1997; Cowan *et al.*, 1997b), and at Mt Bryan O'Lynn, Westland (see Coleman *et al.*, 1980; Coleman *et al.*, 1985; Green and Coleman, 1986), but both were composed of a mixture of podocarp and broadleaved angiosperm trees (Fitzgerald, 1976; Coleman *et al.*, 1980). When it is considered that *Nothofagus* dominated forests comprise 46 % of New Zealand's indigenous forest area (Wardle, 1984), the necessity for a comprehensive study of possum ecology within this forest type is obvious.

Aspects of possum ecology have been studied in *Nothofagus* forests at several sites (Clout and Gaze, 1984; Rose *et al.*, 1993; Owen and Norton, 1995; Pekelharing *et al.*, 1998a; Pekelharing *et al.*, 1998b; Cochrane and Norton, 2000), some of which had floristic similarities with the one studied here. However, the one studied here was unique in that it represented wet *N. fusca* / *N. menziesii* forest containing greater

diversity and abundance of palatable species than other studied *N. fusca / N. menziesii* forests. Much of this palatable species' diversity and abundance was attributable to the presence of the roadside, which formed the greatest floristic discontinuity within the site and the most obvious vegetation type. As such, the distribution of most palatable species was relatively heterogeneous when compared to most of the species commonly found within the forest. However, *W. racemosa* was a notable exception, with a fairly broad distribution throughout the forest and part of the roadside. The lower heterogeneity of forest species and the lack of obvious floristic discontinuities made classification of forest vegetation types difficult, yet steep areas and terrace areas formed reasonably coherent groups despite the fact that floristically transitional areas occurred between them.

Given the heterogeneity of palatable species within the site it would be intuitive to suggest that possum movements were likely to have reflected the distribution of these resources. On average, home ranges and range lengths of the radio-tracked possums were larger than those observed for possums in other continuous forests, yet smaller than those observed for possums in some highly heterogeneous pastoral complexes. However, considerable variability existed in home range size and shape among individuals, with some possums having small ranges with singular core areas and others having large home ranges containing multiple core areas. Furthermore, the locations of home ranges varied markedly with respect to landform and vegetation within the study site, as possums lived at the roadside, on the escarpment adjacent to the northern roadside, on steep sections of the upper central stream and lower hillside, and in the simple terrace areas. Variability between seasons was limited to a larger range size in March/May when compared to July/September. This variability in ranging behaviour suggests that possums were responding to vegetation heterogeneity in both a spatial and temporal sense, although the influence of inherent variability of individuals and social interactions among individuals is difficult to discount.

It is assumed that the primary factor driving possums' response to vegetation heterogeneity is foraging behaviour, which in turn determines diet. The diet of possums within the study site was broadly similar to diet observed in many other forest types within New Zealand. The bulk of the diet comprised few species, yet numerous other food types were consumed in small amounts. *W. racemosa* was the

most consistently consumed species, but it was not simply consumed in proportion to its abundance because it was ranked in the top ten most preferred species for April, August and overall. Other species that ranked in the overall top ten most preferred species, which have also been identified as preferred or highly consumed in other studies, included, in decreasing order of rank, *F. excorticata*, *R. cissoides*, *M. australis* and *T. repens*. The species comprising the top ten most preferred varied markedly among the seasons, with only one species, *Neomyrtus pedunculata*, being preferred in all seasons and four others being preferred in only two seasons. Similarly, the suite of species consumed in each season differed markedly.

Of particular interest was the high overall preference ranking of fruit from *Carpodetus serratus* and *Pseudopanax colensoi*, and the high preference ranking of fruit and flowers from other species in different seasons. These food types, when consumed, generally comprised the bulk of possum stomach contents. When it is considered that the distribution of flowers and fruit is highly patchy, the non-consumption of these food types by some possums may simply reflect effective unavailability. Such behaviour would lead to an underestimation of the preference of these food items when consumption levels are averaged across individuals, as is the traditional approach. Indeed, when food types were averaged for only those possums that consumed them, flowers and fruit became the highest ranking. A similar effect may occur with the consumption of invertebrates and fungi, although their abundance would need to be determined to assess this.

Fundamentally, the issue of variability in possum diet relates to effects of scale, as the choice of what possums can consume is constrained by what is available to them, both temporally and spatially. This issue is an important one when it is considered that calculations of resource preference are heavily dependent on definitions of resource availability. Indeed, preferences were shown to differ markedly with different spatial and temporal definitions of availability in this study. As such, the use of preference ranks, as opposed to absolute values, is to be recommended in order to avoid overstating accuracy (Norbury and Sanson, 1992).

Behavioural variation has been proposed as an adaptive characteristic of possums (Kerle, 1984) and, as such, diet variation is likely an evolved strategy. Possums have

frequently been described as opportunistic feeders and it is likely that variation in diet stems from the interaction between the consumption of a wide array of food types alongside staple food types and the spatiotemporal variability in availability of food types. This behaviour could be viewed as sampling what is on offer at any point in space and time. Such sampling would enable possums to respond quickly to changes in food availability, and therefore provides a mechanism for them to exploit ephemeral food types and 'optimise' their diet.

If this is indeed the case, then the high consumption of fruit, flowers, fungi and invertebrates suggests that these food types represent the most preferred of all. These food types were probably difficult to find, given their patchy distribution, but once found they were commonly consumed almost to the point of exclusion of other food types. The implication is that the more preferred the food item being consumed, the less likely it is that the possum would search for additional food items, as the probability of finding a more desirable food item is low.

The high variability observed in possum diet was also reflected by correlations between possum movements and resource variables. Modelling of cell usage by individuals yielded many significant models, but these varied markedly among individuals and among seasons. Analysis at the second order spatial scale indicated that positive correlations occurred more frequently between individual possum presence and resource variables than negative correlations, which suggests that possums within the study site chose where to live on the basis of preference rather than avoidance. However, all correlations were relatively inconsistent between individuals, suggesting that either individual possums were inherently variable in their choices or that there was inherent variability in the suite of options available to choose from. A positive relationship between diet and possums' presence was implied by the frequency of inclusion of the LnPrefOverall variable, the product of individual log-transformed abundances of the top ten ranked preferred species as defined overall, in models for individual presence at the second order selection scale. This suggests that, although there was latent variability among possums, there was a general trend for possums to be present in areas with abundant preferred species.

Modelling of pooled possum use likely provided the most coherent results because only the strongest and most consistent relationships stood out against the background of individual variability. Such modelling indicated that, on an annual scale, possum use was positively correlated with floristically diverse areas, defined by species richness, and negatively correlated with *N. fusca*, *Coprosma rotundifolia* and *Q. acutifolia* abundance, which are all species unpreferred by possums within the study site (Chapter 5). Similar to the individual models at the second order scale, the LnPrefOverall variable was found to be positively correlated with possum use in the March/May and November/January seasons for the pooled use data at the second order selection scale.

Patterns of selection were less obvious at the third order scale, yet possum use was found to be positively correlated with *C. serratus* abundance for a third of the possums in the March/May season. When it is considered that *C. serratus* was effectively unavailable to several possums within their March/May range, the significance of these correlations is apparent. Because *C. serratus* fruit has been shown to be highly preferred during this season (Chapter 5), these observations, together with the tendency for the LnPrefOverall variable to be included in individual and pooled models at the second order selection scale, provide further evidence to support the contention that possums' space use is indeed influenced by diet preference.

This link between diet preference and space use was not as clearly identified with habitat selection analysis. Overall tests of the choice of home range location (second order) and the use of space within home ranges (third order) indicated that these processes were random, with respect to the classified habitat types. However, overall tests of third order habitat selection approached significance for the March/May and the annual temporal scale. Pairwise habitat type comparisons at the third order selection scale indicated that habitat type three (terrace forest) was significantly preferred over habitat type two (steep areas) for the March/May season, over habitat type one (open areas) for the July/September season and over both for the annual temporal scale. If diet is driving these preferences, then these results are counterintuitive, as habitat type three contains the least palatable vegetation (Chapter 4). This suggests that either possums preferentially utilised habitat three for reasons

other than diet or that it provided better foraging opportunities than predicted, when compared to the other habitat types.

Finally, the link between diet and possum movements was confirmed with analysis of the relationship between home range size and the localised abundance of preferred species. A significant negative relationship was observed between these variables, suggesting that possums living in areas with lower abundance of palatable species range more widely. It is assumed that the abundance of preferred species is a measure of localised forage quality, yet this definition included only vascular plant components of diet. As such, the link between diet and possum space use would likely strengthen with a more comprehensive measure of forage quality. The process that likely drives the relationship between home range size and forage quality, as proposed by the food exploitation hypothesis (FEH) (Larter and Gates, 1994), is the requirement for possums to travel further in order to obtain a sufficient diet when forage quality is lower.

When all of these findings are put into context with each other and findings from other studies, a conceptual model describing spatiotemporal possum resource use within the study site can be proposed. A logical starting point is the birth of an individual possum:

- For the first 8 months of life possums are completely dependent on their mothers (Fletcher and Selwood, 2000) and consequently occupy and mimic their mothers' range.

- Once weaned, juveniles gradually become more independent from their mothers until they disperse when aged between 8 and 24 months (Efford, 1998; Cowan and Clout, 2000). Males tend to range much further than females with long distance movements of several kilometres being common (Clout and Efford, 1984; Ward, 1985; Cowan *et al.*, 1996; Cowan *et al.*, 1997a).

- It has been suggested that factors such as competition for food, den sites and mates influence the decision to settle after dispersion (Cowan, 2000b). Explicit habitat qualities are also likely to exert an influence. The influence of

vegetation heterogeneity on settlement within the Palmer Road site is likely to be minimal, as demonstrated by the lack of clear preferences for the location of possum home ranges (the second order selection scale), with respect to the classified vegetation types and resource variables at all temporal scales.

- However, once settled, possums are likely to show spatiotemporal bias towards certain vegetation types, as demonstrated by the identification of preferences for vegetation types within home ranges (third order selection) at some temporal scales.

- They are also likely to show spatiotemporal bias towards areas with higher abundance of palatable species, as demonstrated by the frequency of inclusion of the LnPrefOverall variable as a positive correlate of possum use of cells at different spatiotemporal scales.

- Nevertheless, possums are unlikely to change the *location* of their home ranges dramatically, as demonstrated by the failure to identify strong bi-monthly shifts in habitat preference or consistent bi-monthly changes in correlations with resource variables. Instead, they are likely to modify the *size* of their home range in order to gain sufficient sustenance from the area in which they have chosen to settle, as demonstrated by the negative relationship between home range size and forage quality.

- The composition of possum diet is constrained by the availability of food within the home range. Possums are reluctant to travel far to obtain specific food types when there are other alternative food types available within the home range. Such behaviour has been observed in other studies where highly palatable species were utilised much less than expected (Thomas *et al.*, 1984). This behaviour explains the high variation in consumption of specific food types among individuals observed in most possum diet studies, as it reflects the vegetation heterogeneity of a site.

High site fidelity by possums has been observed in many other studies (Crawley, 1973; Jolly, 1976; Ward, 1978; Brockie *et al.*, 1989). In particular, Efford *et al.*

(2000) observed a reluctance to dramatically shift ranges despite the removal of neighbouring possums. Such a range shift would likely have conferred a benefit through decreased intraspecific competition between individuals, yet this benefit was not great enough to overcome possums' reluctance to leave their established range.

This behaviour possibly represents a strategy to avoid inbreeding within a population; juvenile males typically disperse far from their natal site and then are unlikely to return, even by chance. In which case, it would be unlikely that possums would have the opportunity to mate with their close relatives.

This goes some way towards explaining why possums within the study site lived in simple terrace areas, which contained low abundance of palatable species, yet never utilised the adjacent roadside, which contained abundant palatable species. Previous control work had decreased the density of possums along the roadside (Appendix 1) and the likelihood of a trade-off between foraging and predation is low (McDonald-Madden *et al.*, 2000), which suggests that foraging efficiency would have been improved if such possums had shifted their ranges in order to utilise the roadside areas. The decision to increase range size as opposed to shifting range location suggests that high site fidelity is fundamental possum behaviour.

6.2 Management implications

Management of possums within New Zealand is very scale dependent. This dependency relates to the fact that possum distribution is variable at multiple scales from regional abundance to individual movements. The importance of scale is related to the drive for efficiency in control and monitoring operations. Operations seek to minimise the delivery of poison or the use of person-hours, or both, whilst still achieving targets for population reduction, conservation management goals or monitoring precision. In the first instance, efficient use of resources requires prioritisation of areas that require control. Once areas have been selected, efficiency can be further improved by identifying the fine-scale distribution of pest species within the environment and tailoring control and monitoring operations to target this spacing (e.g. Thomas *et al.*, 1984; Cowan *et al.*, 1989; Hickling and Thomas, 1990; Moller *et al.*, 1996; Henderson, 1999).

Two facets of this study have implications for a multi-scaled approach to possum management. These are possum movements and resource selection.

6.2.1 Possum movements

Efficiency of control and monitoring operations can be optimised with specific knowledge of the variability of ranging behaviour of the animal in question (Cowan *et al.*, 1989). An important factor for optimising such operations is the interaction between home range size and spacing of control or monitoring devices because this determines the potential frequency of encounter between animal and device. As such, the spacing required for control and monitoring operations should be dictated by their goals and the home range sizes of animals at the sites in question. For example, if the goal is to eradicate possums from an area then each possum must have access to a control device, but if a more general reduction in density is all that is required, then a less intensive, and therefore cheaper, spacing may be sufficient. However, it must be noted that these operations are likely to occur over quite different time periods.

The ranging behaviour identified in this study has implications for operations within similar *Nothofagus* forests. Of particular interest are the three day and bi-monthly range lengths and sizes, as these are the closest temporal scales to those used for most control or monitoring operations (Henderson, 1999; NPCA, 2000). The home ranges observed in this study typically exhibited no consistent shape bias. As such, a regular control grid or control lines of no specific orientation would be sufficient to control possums in this vegetation type.

If eradication is the goal of an operation within a site similar to the one studied here, then control devices would need to be spaced at a density of one per 2 ha, the minimum mean bi-monthly home range out of all individuals, assuming that such an operation would span at least several months. However, for more common short-term operations, three-day home range should be used as the basis of device spacing. In this case, if all possums are to have a probability of capture, devices should be spaced at a ratio of one per hectare, but if all that is required is that most possums have a probability of capture then devices only need to be spaced at a ratio of one per 2-3 ha.

The effect of season on home range size is worthy of mention because of the effect of home range size on probability of encounter between possum and control or monitoring device. Smallest home ranges in this study were observed to occur during winter. It has been suggested that the efficacy of poisoning is highest at this time of the year (Henderson, 1999), but the smaller range sizes at this time may create a trade-off by reducing the encounter rate between possum and device.

Differences in home range sizes may also have implications for the residual trap catch (RTC) method of possum monitoring. RTC is the favoured index of possum density within New Zealand for both conservation and Tb vector control (Warburton, 2000), and, given its extensive use, considerable steps have been taken to standardise this approach (NPCA, 2000). Given that ranging behaviour governs the likelihood of encounter of possum and trap, under a standardised spacing regime the comparability of different RTC values between areas with different home range sizes is called into question. For example, it could be argued that possums have a greater likelihood of trap encounter in *Nothofagus* forest than they do in mixed podocarp / broadleaved angiosperm forest due to the differences in home range in these vegetation types. If so, the RTC indices (indices of absolute density) obtained from such sites are likely to have greater similarity than the absolute densities of the possum populations.

Fundamentally, this problem is forage quality dependent, as demonstrated by the negative relationship between forage quality and home range size. Viewed in this way, another related problem becomes apparent; comparisons between pre-control and post-control RTC indices may be influenced by forage quality. Unless the time lapse between monitoring operations is short, forage quality is likely to be better during post-control RTC monitoring due to a reduction in herbivory. As such, possum home ranges are likely to be smaller and the likelihood of possums encountering traps lower than for the pre-control monitoring. This may provide an overestimate of the success of a control operation, but is completely dependent on the extent of home range change.

6.2.2 Resource selection

Although considerable focus is given to fine scale influences on possum control and monitoring, broader regional or landscape scales also provide many opportunities to improve efficiency of such operations.

Stratification is a technique applied to both control and monitoring operations and has the potential to improve overall precision and economy (McCallum, 2000). Habitat selection analyses provide a method to determine whether or not an area would be suitable to stratify, as such analyses indicate a bias in preference for habitat types, which can then be translated into a bias in control or monitoring intensity. In this study, no consistent preference was shown for the classified vegetation types, which suggests that the study site should be treated as a single management unit for control and monitoring purposes. Such an outcome provides valuable insights into the level of heterogeneity required to make stratification worthwhile.

Stratification on a larger, regional scale would provide a useful tool for possum managers and could be facilitated by modelling approaches. Although the modelling within this study was fine-scale, there is scope to integrate it with other, more coarse-scale modelling in order to obtain a more comprehensive understanding of resource use by possums (e.g. Mackey and Lindenmayer, 2001). Once developed, such models would allow managers to identify patterns of potential possum density across regions. They may also be able to identify patchiness on a finer scale, given an adequate resolution of environmental data.

6.3 Further research

Throughout the investigation of possum resource selection in this study several, sometimes inter-related, questions have been posed or implied. These are outlined as follows:

- What effect does home range size have on RTC indices? If RTC indices are strongly influenced by home range size then there is an inherent flaw in the information being obtained by many possum managers. In this case there may

be merit in defining specific trap spacing for generic forest types, which could be achieved with investigation of the relationship between home range size, RTC and absolute density in various vegetation types. Clearly, the standardised procedure used for RTC allows consistency between operators. However, consistency between operations should also be a requirement in order for managers to make robust decisions on what areas require control.

- How can we obtain average consumption levels of food items by individuals in the field? Non-destructive methods for diet analysis would be very useful because stomach samples are instantaneous samples and therefore frequently provide numerous zero values for food items that may not have been consumed purely by chance. Faecal analysis suffers from uneven digestion rates of food types and live sampling of stomach contents, used for some large herbivores, is difficult for use on wild animals (Holechek *et al.*, 1982) and would likely be unsuitable for possums, given their size.

- What are the relative preferences for non-foliar food types? Considering the importance of these food types in possum diet it would be useful to have an idea of the relationship between their abundance and their consumption levels. Such investigation would be of benefit as it would lead to a more comprehensive understanding of possums' preferences.

- How do we define resource quality for possums? Having a better understanding of resource quality may provide a better understanding of variation in density and home range size, which have numerous implications for possum management. This question would be supported by question three and would require investigation of the primary factors governing individual possum survival or fitness.

- How do we define resource availability? An approach motivated by optimal foraging theory would require investigations into the costs incurred by foraging possums. Outcomes of such investigation may make availability estimates more spatially explicit, which would provide a refinement for current resource selection techniques.

Many of these questions are complementary and could potentially be combined in a comprehensive resource selection study.

A common theme within this study has been the importance of scale. Possums have been described as highly variable animals and it is probable that most of this variability is a reflection of the spatiotemporal variability in the abiotic and biotic environment. A major challenge for future possum management within New Zealand will be elucidating the role that this scale-dependent variability plays in possum resource selection, because doing so may provide a basis for increasing the efficacy of management of this serious pest.

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Appendix 1: Density Estimate

Density is arguably the most important population parameter when defining the state of a population. Density dictates the level of competition for resources and mates and, therefore, strongly influences mortality and fecundity (Begon *et al.*, 1996). Because density has such an influential effect on the way animals interact with each other, and the way they utilise their surrounding environment, it is important to provide a measure of density when dealing with resource selection studies.

There are several ways to obtain measures of density but density indices are by far the easiest to obtain. Density indices are correlates of absolute density, and prove useful when comparing between temporally segregated measurements in long-term studies, or comparing between spatially segregated areas that are deemed to share the same proportionality between the index and absolute density (McCallum, 2000). However, they have limited use for comparisons when this proportionality differs, which is often the case when dealing with widely separated areas and populations. It is therefore necessary to include an estimate of absolute possum density in the study area at the time of study in order to provide a more robust context with which to compare this study with others.

A Department of Conservation possum control operation provided an opportunity to collect trapping and poisoning data from the study area, which was used to provide an estimate of density. The control operation was undertaken by a team of experienced possum control contractors after the conclusion of the radio-tracking data collection outlined in this thesis. Victor® no.1 leg-hold traps were laid initially for several days along trap lines throughout the study site and also further along the terrace for approximately 1 km from the south-western boundary of the study site. Trap-lines were operational for three to four consecutive nights. Possum numbers were found to be evenly spread throughout the entire control area (Bygate, 2001), therefore density estimates derived for the entire control area can be applied to the study site. As a follow-up to trapping, poison was laid along trap-lines in order to kill any remaining trap shy individuals at the end of the control period. In total 139 possums were killed; 101 from traps and 38 from poison.

In order to define the absolute density, the effective trapping area must be calculated (Efford, 2000). The effective trapping area was defined as the area encompassed by a buffer around the trapping lines equal to half the average width of the radio-tracked possums' three-day home ranges, as calculated using the kernel method. The classification of the effective trapping area using this method yielded an estimate of 200 ha.

Two different methods were used to derive a suitable estimate of absolute density: these include a method combining the index-manipulation-index and mark/recapture methods, and absolute density estimation from trap-catch calibration. These are outlined as follows:

Index-manipulation-index and mark/recapture:

The size of a closed population can be estimated by measuring a linear density index value before and after a manipulation of the population (Caughley, 1977). The size of the population before manipulation is given by:

$$N = \frac{I_1 C}{I_2 - I_1}$$

Where N is population size, I_1 is the index value before removal, I_2 is the index value after removal and C is the change of individuals (Riney, 1957).

Although the population at the study site is not closed, it could be considered as approximating a closed population for this estimate of density because the period of time between the measurement of indices and population manipulation is short, and the shift of possum home range after control is relatively slow (Efford *et al.*, 2000).

The ratio of catches per trap (trap-catch) is a linear index of absolute density for values less than 0.2 (Caughley, 1977). However, on some of the trap-lines the initial trap-catch exceeded 0.2, therefore the trap-catch needed to be converted to an estimated density of catches per trap, which is a completely linear index of absolute density (Caughley, 1977). The effective population estimate of trap-prone possums was calculated separately for each trap-line and was then summed across lines to obtain an effective population estimate of trap-prone possums for the effective

trapping area. These calculations yielded an estimate of 144 trap-prone possums for the entire trapping area.

After the bulk of the trapping had taken place, poison was laid in pre-fed bait stations along previously established trapping lines in order to kill trap-shy possums. This yielded a further 38 possums, only two of which were collared individuals. Because the total number of radio-collared (marked) possums in the effective trapping area was known immediately prior to the control operation, this situation can be treated as a mark/recapture experiment and can be used to estimate the residual trap-shy possum population (Caughley, 1977; McCallum, 2000). Recent radio-tracking had revealed a total of six collared possums in the effective trapping area before the control operation commenced. None were caught in traps, which indicated trap-shyness.

In mark/recapture experiments, the proportion of marked animals in the sample of recaught or resighted animals is deemed to approximate the proportion of all the marked animals in the total population (Caughley, 1977; McCallum, 2000); this is the Lincoln-Peterson model. The assumptions of this model are not entirely satisfied in this situation, as the population is not closed, however, the short period of time between the confirmation of collared possums in the area and the population sampling (poisoning) renders the population effectively closed where this study is concerned. The assumption of non-differing catchability between marked and unmarked animals holds true for this approach as the marked possums were caught in traps, whereas the final sample was obtained with poison; avoiding the potential problem of trap-shyness.

A problem did exist due to the uneven distribution of marked possums throughout the trapping area, which is likely to lead to an overestimate of numbers. However, previous radio-tracking revealed that the marked possums were evenly distributed throughout the north-eastern half of the effective trapping area, which allows for some correction of the bias. If the poisoned possums are assumed to have been evenly distributed throughout the effective trapping area, then the population of possums in the northern half of the effective trapping area can be dealt with in isolation. The sample of poisoned possums is halved when used in the Lincoln-Peterson model, and

then the yielded north-eastern population estimate is doubled to give the overall population estimate.

The Lincoln-Peterson model adapted to avoid the bias of small numbers of marked animals in the final sample (McCallum, 2000) is given by:

$$N = \frac{(n_1 + 1)(n_2 + 1)}{r + 1} - 1$$

Where N is the estimated population size, n_1 is the number of animals in the original sample that are consequently marked, n_2 is the total number of animals in the final sample and r is the number of marked animals in the final sample. When the values obtained from the poisoning operation are substituted into the equation, a population estimate of 90 possums is obtained for the effective trapping area at the conclusion of trapping.

Combining the estimates of the trap-prone and trap-shy possum populations gives a total population estimate for the 200 ha trapping area of 234 possums, which yields an estimated absolute density of 1.2 possums/ha in the study area.

Absolute density estimation from trap-catch calibration:

Batcheler *et al.* (1967) devised a conversion equation which allows the absolute possum density at any lowland site in New Zealand to be estimated from trap-catch frequency data. If the initial trap-catch frequency and the absolute density are know explicitly for the same site within a short time period, then the relationship between the two can be applied to initial trap-catch frequencies at other sites in order to obtain estimates of absolute density (Batcheler *et al.*, 1967). However, this approach relies heavily upon the tenuous assumptions that home range size and probability of capture are constant (Efford, 2000). The conversion equation is expressed as:

$$D = \frac{260Log(1 - F/100)}{698Log(1 - 0.0919)} \times \frac{10000}{4047}$$

Where D is number of possums per hectare and F is the initial trap-catch frequency.

To improve precision a stratified approach was adopted (McCallum, 2000) where the effective trapping area was divided into a roadside stratum, a streamside stratum and a terrace stratum. The initial trap-catch frequency was then calculated for each

individual trap-line and then averaged within strata. An overall initial trap-catch frequency was then calculated by multiplying the average initial trap-catch for each stratum by a weighting factor (the proportion of the effective trapping area in each stratum) and then summing across strata. This method yielded an absolute density estimate of 1.8 possums/ha.

The probability of capture for low-density populations is less than for higher density populations (Batcheler *et al.*, 1967), which suggests that there would be an underestimate of density of the undoubtedly less-dense Palmer Road population. However, this bias may be counteracted by larger home ranges of the Palmer Road population (Chapter 3), which would mean that possums at this site would have a higher exposure to traps and, therefore, a higher probability of capture.

The two estimates of absolute density do not differ markedly and therefore an average of the two (1.5 possums/ha) is likely to be a suitable estimate of absolute density of possums in the study area.

This figure compares well to other estimates of density obtained for possum populations around the country. It is considerably lower than most of those reported for mixed podocarp/broadleaf forests and pastoral habitats, but it is slightly higher than densities reported for other *Nothofagus* forests (Efford, 2000). The most robust assessment of the absolute possum density in a *Nothofagus* forest, published to date, yielded a density of 0.5 possums/ha (Clout and Gaze, 1984). This site was at a higher altitude and received lower rainfall than the Palmer Road site and did not contain any significant forest edge areas (Clout and Gaze, 1984). It is likely that the Palmer Road study site offers better forage quality because of the extensive roadside areas containing *T. repens*, *A. serrata, M. australis* and *F. excorticata,* and because of the abundant *Weinmannia racemosa* on the upper terraces and lower slopes of the hill. This difference in forage quality and climate is likely to be responsible for the higher density of possums at the Palmer Road study site.

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Appendix 2: Species codes, botanical names and common names.

Species code	Botanical name	Common name
ACASPP	*Acaena* species	Bidibid
AGRCAP	*Agrostis capilliaris*	Brown top
ANISPP	*Anisotome* species	
ARISER	*Aristotelia serrata*	Wineberry
ASPBUL	*Asplenium bulbiferum*	Hen and chicken fern
ASPFLA	*Asplenium flaccidum*	Hanging spleenwort
ASTFRA	*Astelia fragrans*	Kakaha
BLECHA	*Blechnum chambersii*	Lance fern
BLECOL	*Blechnum colensoi*	Paretako
BLEDIS	*Blechnum discolour*	Crown fern
BLEFLU	*Blechnum fluviatile*	Kiwakiwa
BLEMIN	*Blechnum minus*	Swamp kiokio
BLENOV	*Blechnum novae-zelandiae*	Kiokio
BLEPEN	*Blechnum penna-marina*	Little hard fern
BLEPRO	*Blechnum procerum*	Small kiokio
BLEVUL	*Blechnum vulcanicum*	Triangular kiokio
CARDSP	*Cardamine* species	
CARSEC	*Carex secta*	Makura
CARSER	*Carpodetus serratus*	Putaputaweta
CARSPP	*Carex* species	
CIRSPP	*Cirsium* species	Thistle
COPCOL	*Coprosma colensoi*	
COPFOE	*Coprosma foetidissima*	Stinkwood
COPLUC	*Coprosma lucida*	Shining karamu
COPMIC	*Coprosma microcarpa*	
COPPAR	*Coprosma parviflora*	
COPPRO	*Coprosma propinqua*	Miki
COPPSE	*Coprosma pseudocuneata*	

COPPXR	*Coprosma propinqua* x *robusta*	
COPRHA	*Coprosma rhamnoides*	
COPROT	*Coprosma rotundifolia*	Round-leaved comprosma
CORRIC	*Coriaria richardii*	Toitoi
CYACOL	*Cyathea colensoi*	Mountain tree fern
CYASMI	*Cyathea smithii*	Ponga
DICSQU	*Dicksonia squarosa*	Rough tree fern
DIGPUR	*Digitalis purpurea*	Foxglove
ELAHOO	*Eleaocarpus hookerianus*	Pokaka
FUCEXC	*Fuchsia excorticata*	Kotukutuku
GAURUP	*Gaultheria rupestrus*	
GNAAUD	*Gnaphalium audax*	
GRILIT	*Griselinia littoralis*	Broadleaf
HEBSAL	*Hebe salicifolia*	Koromiko
HELBEL	*Helichrysum bellidioides*	
HIESPP	*Hieracium* species	Mouse ear hawkweed
HISINC	*Histiopteris incisa*	Water fern
HOLLAN	*Holcus lanatus*	Yorkshire fog
HYDSPP	*Hydrocotyle* species	Penny wort
HYPMIL	*Hypolepis millefolium*	Thousand leaved fern
HYPRAD	*Hypocheoris radicata*	Catsear
HYPRUF	*Hypolepis rufobarbata*	
ISOHAB	*Isolepis habra*	
JUNSPP	*Juncus* species	Rush
LAGSPP	*Lagenifera* species	
LEPHYM	*Leptopteris hymenophylloides*	Heruheru
LEPSUP	*Leptopteris superba*	Prince of Wales' feathers fern
LEUFAS	*Leucopogon fasciculatus*	Mingimingi
LOTPED	*Lotus pedunculata*	Lotus
LUZSPP	*Luzula* species	Woodrush
LYCSCA	*Lycopodium scariosum*	Creeping clubmoss
MELLAN	*Melicytus lanceolatus*	Kaiweta
METDIF	*Metrosideros diffusa*	White rata

METUMB	*Metrosideros umbellata*	Southern rata
MICAVE	*Microlaena avenacea*	Bush rice grass
MUEAUS	*Muehlenbeckia australis*	Pohuehue
MYRDIV	*Myrsine divaricata*	Weeping mapou
NASOFF	*Nasturtium officinale*	Water cress
NEOPED	*Neomyrtus pedunculata*	Rohutu
NERDEP	*Nertera depressa*	
NERVIL	*Nertera villosa*	
NOTFUS	*Nothofagus fusca*	Red beech
NOTMEN	*Nothofagus menziesii*	Silver beech
PENCOR	*Pennantia corymbosa*	Kaikomako
PERCOL	*Peraxilla colensoi*	Mistletoe
PERTET	*Peraxilla tetrapetela*	Mistletoe
PHYDIV	*Phymatosorus diversifolia*	Hounds tongue
PITCOL	*Pittosporum colensoi*	Rautawhiri
PITEUG	*Pittosporum eugenioides*	Lemonwood
PITTEN	*Pittosporum tenuifolium*	Kohuhu
PNEPEN	*Pneumatopteris pennigera*	Gully fern
POLVES	*Polystichum vestitum*	Shield fern
PRUFER	*Prumnopitys ferruginea*	Miro
PRUVUL	*Prunella vulgaris*	Self-heal
PSEARB	*Pseudopanax arboreus*	Five-finger
PSECOL	*Pseudowintera colorata*	Horopito
PSECON	*Pseudopanax colensoi*	Three-finger
PSECRA	*Pseudopanax crassifolius*	Lancewood
QUIACU	*Quintinia acutifolia*	Quintinia
RANREP	*Ranunculus repens*	Buttercup
RAUANO	*Raukaua anomalous*	
RAUSIM	*Raukaua simplex*	Haumakaroa
RUBCIS	*Rubus cissoides*	Bush lawyer
RUBSCH	*Rubus schmidelioides*	Bush lawyer
RUMACE	*Rumex acetosa*	Sheep sorel
SCHDIG	*Schefflera digitata*	Pate

SENJAC	*Senecio jacobaea*	Ragwort
TARSPP	*Taraxacum* species	Dandilion
TRIREP	*Trifolium repens*	White clover
UNCSPP	*Uncinia* species	Hook grass
URTINC	*Urtica incisa*	Stinging nettle
WEIRAC	*Weinmannia racemosa*	Kamahi

Appendix 3: Descriptions of all resource variables

Resource variable	Description
SR	Species richness.
COVER	Canopy cover.
SDI	Shannon diversity index.
Tier1	Summed importance values of all species in the canopy tier.
Tier2	Summed importance values of all species in the sub-canopy tier.
Tier3	Summed importance values of all species in the shrub tier.
Tier4	Summed importance values of all species in the ground tier.
TierTOT	Summed importance values of all species in all tiers.
Seral	Summed importance values of all seral species.
Herb/Grass	Summed importance values of all herb and grass species.
Ferns	Summed importance values of all fern species.
Shrub	Summed importance values of all shrub species.
Vines	Summed importance values of all vine species.
PrefAPR	Summed importance values of the top ten most preferred species defined from the April diet sample.

PrefAUG	Summed importance values of the top ten most preferred species defined from the August diet sample.
PrefDEC	Summed importance values of the top ten most preferred species defined from the December diet sample.
PrefOverall	Summed importance values of the top ten most preferred species defined from the overall diet sample.
PrefCondit	Summed importance values of the top ten most preferred species defined from the overall diet sample when species preference is averaged only for those possums that consumed that species.
LnPrefAPR	Summed log-transformed importance values of the top ten most preferred species defined from the April diet sample.
LnPrefAUG	Summed log-transformed importance values of the top ten most preferred species defined from the August diet sample.
LnPrefDEC	Summed log-transformed importance values of the top ten most preferred species defined from the December diet sample.
LnPrefOverall	Summed log-transformed importance values of the top ten most preferred species defined from the overall diet sample.
LnPrefCondit	Summed log-transformed importance values of the top ten most preferred species defined from the overall diet sample when species preference is averaged only for those possums that consumed that species.

Appendix 4: Correlation coefficients for species with frequencies of 25% or greater overall.

Pearson Correlation Coefficients, N = 277
Prob > |r| under H0: Rho=0

	ARISER	BLEDIS	BLEFLU	BLENOV	CARSER	COPFOE	COPPAR	COPRHA	CYACOL	CYASMI	DICSQU	GRILIT	HISINC	MICAVE
ARISER	1.00000	-0.22961 0.0001	0.15069 0.0120	0.20150 0.0007	0.05378 0.3726	0.09640 0.1094	0.19309 0.0012	0.03661 0.5441	0.10826 0.0720	-0.05963 0.3227	-0.02089 0.7293	0.02196 0.7159	0.09686 0.1077	0.12605 0.0360
BLEDIS	-0.22961 0.0001	1.00000	0.28110 <.0001	0.07210 0.2317	-0.10437 0.0829	0.13875 0.0209	0.17963 0.0027	0.20159 0.0007	0.29450 <.0001	-0.02261 0.7079	-0.09920 0.0994	0.14104 0.0188	0.00864 0.8862	0.15141 0.0116
BLEFLU	0.15069 0.0120	0.28110 <.0001	1.00000	0.76615 <.0001	0.21772 0.0003	0.63597 <.0001	0.78313 <.0001	0.73721 <.0001	0.84828 <.0001	0.21683 0.0003	0.06877 0.2540	0.33622 <.0001	0.61078 < .0001	0.80533 <.0001
BLENOV	0.20150 0.0007	0.07210 0.2317	0.76615 <.0001	1.00000	0.22049 0.0002	0.56574 <.0001	0.58269 <.0001	0.55822 <.0001	0.63248 <.0001	0.08375 0.1645	0.02396 0.6914	0.17800 0.0030	0.42506 <.0001	0.59664 <.0001
CARSER	0.05378 0.3726	-0.10437 0.0829	0.21772 0.0003	0.22049 0.0002	1.00000	0.15625 0.0092	0.14474 0.0159	0.20592 0.0006	0.15198 0.0113	0.16658 0.0054	0.54083 <.0001	0.41413 <.0001	0.25102 <.0001	0.15587 0.0094
COPFOE	0.09640 0.1094	0.13875 0.0209	0.63597 <.0001	0.56574 <.0001	0.15625 0.0092	1.00000	0.62400 <.0001	0.53865 <.0001	0.55712 <.0001	0.04288 0.4772	-0.01144 0.8497	0.14007 0.0197	0.30280 <.0001	0.50573 <.0001
COPPAR	0.19309 0.0012	0.17963 0.0027	0.78313 <.0001	0.58269 <.0001	0.14474 0.0159	0.62400 <.0001	1.00000	0.67055 <.0001	0.75302 <.0001	0.11956 0.0468	0.00841 0.8892	0.32241 <.0001	0.43313 <.0001	0.65290 <.0001
COPRHA	0.03661 0.5441	0.20159 0.0007	0.73721 <.0001	0.55822 <.0001	0.20592 0.0006	0.53865 <.0001	0.67055 <.0001	1.00000	0.63376 <.0001	0.10878 0.0707	-0.01863 0.7575	0.38983 <.0001	0.38949 <.0001	0.63868 <.0001
CYACOL	0.10826 0.0720	0.29450 <.0001	0.84828 <.0001	0.63248 <.0001	0.15198 0.0113	0.55712 <.0001	0.75302 <.0001	0.63376 <.0001	1.00000	0.10790 0.0730	0.03467 0.5656	0.34792 <.0001	0.50380 <.0001	0.71686 <.0001
CYASMI	-0.05963 0.3227	-0.02261 0.7079	0.21683 0.0003	0.08375 0.1645	0.16658 0.0054	0.04288 0.4772	0.11956 0.0468	0.10878 0.0707	0.10790 0.0730	1.00000	-0.01916 0.7508	-0.04742 0.4318	0.09772 0.1046	0.10348 0.0856
DICSQU	-0.02089 0.7293	-0.09920 0.0994	0.06877 0.2540	0.02396 0.6914	0.54083 <.0001	-0.01144 0.8497	0.00841 0.8892	-0.01863 0.757 5	0.03467 0.5656	-0.01916 0.7508	1.00000	0.57780 <.0001	0.28343 <.0001	0.03647 0.5456
GRILIT	0.02196 0.7159	0.14104 0.0188	0.33622 <.0001	0.17800 0.0030	0.41413 <.0001	0.14007 0.0197	0.32241 <.0001	0.38983 <.0001	0.34792 <.0001	-0.04742 0.4318	0.57780 <.0001	1.00000	0.30083 <.0001	0.32664 <.0001
HISINC	0.09686 0.1077	0.00864 0.8862	0.61078 <.0001	0.42506 <.0001	0.25102 <.0001	0.30280 <.0001	0.43313 <.0001	0.38949 <.0001	0.50380 <.0001	0.09772 0.1046	0.28343 <.0001	0.30083 <.0001	1.00000	0.46712 <.0001
MICAVE	0.12605 0.0360	0.15141 0.0116	0.80533 <.0001	0.59664 <.0001	0.15587 0.0094	0.50573 <.0001	0.65290 <.0001	0.63868 <.0001	0.71686 <.0001	0.10348 0.0856	0.03647 0.5456	0.32664 <.0001	0.46712 <.0001	1.00000

Pearson Correlation Coefficients, N = 277
Prob > |r| under H0: Rho=0

	MUEAUS	MYRDIV	NEOPED	NERVIL	NOTFUS	NOTMEN	PSECOL	PSECRA	QUIACU	RAUANO	RAUSIM	RUBCIS	UNCSPP	WEIRAC
ARISER	0.28281 <.0001	-0.00758 0.9001	-0.12038 0.0453	0.13950 0.0202	-0.33686 <.0001	-0.14978 0.0126	-0.06739 0.2636	0.16592 0.0056	-0.12107 0.0441	0.00741 0.9022	-0.09079 0.1317	0.20449 0.0006	0.15940 0.0079	-0.18799 0.0017
BLEDIS	0.15375 0.0104	0.19165 0.0014	0.16584 0.0057	0.31793 <.0001	0.51915 <.0001	0.33628 <.0001	0.06729 0.2644	0.11465 0.0567	-0.03518 0.5599	-0.06839 0.2566	0.33192 <.0001	-0.03528 0.5587	0.18990 0.0015	-0.12089 0.0444
BLEFLU	0.87639 <.0001	0.48779 <.0001	0.00182 0.9760	0.99592 <.0001	-0.11299 0.0604	-0.04766 0.4294	0.05701 0.3445	0.53698 <.0001	-0.02712 0.6531	0.13886 0.0208	0.36045 <.0001	0.35657 <.0001	0.91892 <.0001	-0.02235 0.7111
BLENOV	0.68374 <.0001	0.34638 <.0001	-0.06303 0.2959	0.75733 <.0001	-0.15631 0.0092	-0.12005 0.0459	-0.02826 0.6396	0.48350 <.0001	0.00940 0.8763	0.09322 0.1217	0.28915 <.0001	0.51180 <.0001	0.70083 <.0001	0.08784 0.1448
CARSER	0.22926 0.0001	0.09344 0.1208	-0.10563 0.0793	0.20651 0.0005	-0.22964 0.0001	-0.14393 0.0165	0.09351 0.1205	0.23331 <.0001	-0.10627 0.0774	-0.01695 0.7788	-0.11561 0.0546	0.19099 0.0014	0.22270 0.0002	-0.01138 0.8 504
COPFOE	0.53409 <.0001	0.34346 <.0001	0.05655 0.3484	0.63756 <.0001	-0.01278 0.8323	-0.04047 0.5024	-0.00980 0.8711	0.36979 <.0001	0.00344 0.9545	0.09929 0.0991	0.30825 <.0001	0.34073 <.0001	0.54674 <.0001	0.05827 0.3339
COPPAR	0.69169 <.0001	0.43690 <.0001	0.00577 0.9239	0.78395 <.0001	-0.13011 0.0304	0.00071 0.9906	0.05533 0.3589	0.52306 <.0001	-0.14517 0.0156	0.18379 0.0021	0.22722 0.0001	0.32167 <.0001	0.71138 <.0001	-0.16494 0.0059
COPRHA	0.75124 <.0001	0.47811 <.0001	-0.00326 0.9570	0.74066 <.0001	-0.00712 0.9061	0.00556 0.9266	0.13023 0.0302	0.57744 <.0001	-0.09328 0.1214	0.12219 0.0421	0.21648 0.0003	0.49028 <.0001	0.67782 <.0001	-0.06897 0.2526
CYACOL	0.78346 <.0001	0.48163 <.0001	0.01600 0.7910	0.85355 <.0001	-0.03597 0.5511	-0.00717 0.9054	0.09308 0.1222	0.52921 <.0001	-0.07477 0.2148	0.15729 0.0087	0.34594 <.0001	0.26894 <.0001	0.76616 <.0001	-0.10678 0.0760
CYASMI	0.15487 0.0098	0.03838 0.5247	-0.10589 0.0785	0.17501 0.0035	-0.22532 0.0002	-0.14747 0.0140	0.33173 <.0001	-0.02133 0.7237	-0.08909 0.1392	-0.04317 0.4742	-0.08333 0.1666	0.01699 0.7784	0.21422 0.0003	0.10174 0.0910
DICSQU	0.02967 0.6230	-0.02120 0.7254	-0.05216 0.3871	0.07000 0.2456	-0.16797 0.0051	-0.07055 0.2419	-0.02011 0.7389	0.12177 0.0429	-0.05280 0.3814	-0.01753 0.7714	-0.07556 0.2100	0.02171 0.7191	0.05281 0.3813	-0.08059 0.1811
GRILIT	0.38277 <.0001	0.29507 <.0001	0.02014 0.7386	0.35051 <.0001	0.03315 0.5828	0.18740 0.0017	0.18225 0.0023	0.51574 <.0001	-0.20048 0.0008	0.00764 0.8993	0.05749 0.3405	0.17198 0.0041	0.30290 <.0001	-0.31254 <.0001
HISINC	0.50822 <.0001	0.28411 <.0001	-0.07896 0.1901	0.60399 <.0001	-0.31771 <.0001	-0.17691 0.0031	-0.02087 0.7295	0.31138 <.0001	-0.07975 0.1857	0.11372 0.0587	0.07620 0.2061	0.25062 <.0001	0.53699 <.0001	-0.09309 0.1222
MICAVE	0.76924 <.0001	0.46782 <.0001	-0.02735 0.6504	0.81252 <.0001	0.04220 0.4842	-0.02872 0.6342	0.28729 <.0001	0.50331 <.0001	-0.08747 0.1465	0.23455 <.0001	0.20381 0.0006	0.27264 <.0001	0.73627 <.0001	-0.13308 0.0268

Pearson Correlation Coefficients, N = 277
Prob > |r| under H0: Rho=0

	ARISER	BLEDIS	BLEFLU	BLENOV	CARSER	COPFOE	COPPAR	COPRHA	CYACOL	CYASMI	DICSQU	GRILIT	HISINC	MICAVE
MUEAUS	0.28281 <.0001	0.15375 0.0104	0.87639 <.0001	0.68374 <.0001	0.22926 0.0001	0.53409 <.0001	0.69169 <.0001	0.75124 <.0001	0.78346 <.0001	0.15487 0.0098	0.02967 0.6230	0.38277 <.0001	0.50822 <.0001	0.76924 <.0001
MYRDIV	-0.00758 0.9001	0.19165 0.0014	0.48779 <.0001	0.34638 <.0001	0.09344 0.1208	0.34346 <.0001	0.43690 <.0001	0.47 811 <.0001	0.48163 <.0001	0.03838 0.5247	-0.02120 0.7254	0.29507 <.0001	0.28411 <.0001	0.46782 <.0001
NEOPED	-0.12038 0.0453	0.16584 0.0057	0.00182 0.9760	-0.06303 0.2959	-0.10563 0.0793	0.05655 0 .3484	0.00577 0.9239	-0.00326 0.9570	0.01600 0.7910	-0.10589 0.0785	-0.05216 0.3871	0.02014 0.7386	-0.07896 0.1901	-0.02735 0.6504
NERVIL	0.13950 0.0202	0.31793 <.0001	0.99592 <.0001	0.75733 <.0001	0.20651 0.0005	0.63756 <.0001	0.78395 <.0001	0.74066 <.0001	0.85355 <.0001	0.17501 0.0035	0.07000 0.2456	0.3505 1 <.0001	0.60399 <.0001	0.81252 <.0001
NOTFUS	-0.33686 <.0001	0.51915 <.0001	-0.11299 0.0604	-0.15631 0.0092	-0.22964 0.0001	-0.01278 0.8323	-0.13011 0.0304	-0.00712 0.9061	-0.03597 0.5511	-0.22532 0.0 002	-0.16797 0.0051	0.03315 0.5828	-0.31771 <.0001	0.04220 0.4842
NOTMEN	-0.14978 0.0126	0.33628 <.0001	-0.04766 0.4294	-0.12005 0.0459	-0.14393 0.0165	-0.04047 0.5024	0.00071 0.9906	0.00556 0.9266	-0.00717 0.9054	-0.14747 0.0140	-0.07055 0.2419	0.18740 0.0017	-0.17691 0.0031	-0.02872 0.6342
PSECOL	-0.06739 0.2636	0.06729 0.2644	0.05701 0.3445	-0.02826 0.6396	0.09351 0.1205	-0.00980 0.8711	0.05533 0.3589	0.13023 0.0302	0.09308 0.1222	0.33173 <.0001	-0.02011 0.7389	0.18225 0.0023	-0.02087 0.7295	0.28729 <.000 1
PSECRA	0.16592 0.0056	0.11465 0.0567	0.53698 <.0001	0.48350 <.0001	0.23331 <.0001	0.36979 <.0001	0.52306 <.0001	0.57744 <.0001	0.52921 <.0001	-0.02133 0.7237	0.12177 0.0429	0.51574 <.0001	0.31138 <.0001	0.50331 <.0001
QUIACU	-0.12107 0.0441	-0.03518 0.5599	-0.02712 0.6531	0.00940 0.8763	-0.10627 0.0774	0.00344 0.9545	-0.14517 0.0156	-0.09328 0.1214	-0.07477 0.2148	-0.08909 0.1392	-0.05280 0.3814	-0.20048 0.0008	-0.07975 0.1857	-0.08747 0.1465
RAUANO	0.00741 0.9022	-0.06839 0.2566	0.13886 0.0208	0.09322 0.1217	-0.01695 0.7788	0.09929 0.0991	0.18379 0.0021	0.12219 0.0421	0.15729 0.0087	-0.04317 0.4742	-0.01753 0.7714	0.00764 0.8993	0.11372 0.0587	0.23455 <.0001
RAUSIM	-0.09079 0.1317	0.33192 <.0001	0.36045 <.0001	0.28915 <.0001	-0.11561 0.0546	0.30825 <.0001	0.22722 0.0001	0.21648 0.0003	0.34594 <.0001	-0.08333 0.1666	-0.07556 0.2100	0.05749 0.3405	0.07620 0.2061	0.20381 0.0006
RUBCIS	0.20449 0.0006	-0.03528 0.5587	0.35657 <.0001	0.51180 <.0001	0.19099 0.0014	0.34073 <.0001	0.32167 <.0001	0.49028 <.0001	0.26894 <.0001	0.01699 0.7784	0.02171 0.7191	0.17198 0.0041	0.25062 <.0001	0.27264 <. 0001
UNCSPP	0.15940 0.0079	0.18990 0.0015	0.91892 <.0001	0.70083 <.0001	0.22270 0.0002	0.54674 <.0001	0.71138 <.0001	0.67782 <.0001	0.76616 <.0001	0.21422 0.0003	0.05281 0.3813	0.30290 <.0001	0.53699 <.0001	0.73627 <.0001
WEIRAC	-0.18799 0.0017	-0.12089 0.0444	-0.02235 0.7111	0.08784 0.1448	-0.01138 0.8504	0.05827 0.3339	-0.16494 0.0059	-0.06897 0.2526	-0.10678 0.0760	0.10174 0.0910	-0.08059 0.1811	-0.31254 <.0001	-0.09309 0.1222	-0.13308 0.0268

Pearson Correlation Coefficients, N = 277
Prob > |r| under H0: Rho=0

	MUEAUS	MYRDIV	NEOPED	NERVIL	NOTFUS	NOTMEN	PSECOL	PSECRA	QUIACU	RAUANO	RAUSIM	RUBCIS	UNCSPP	WEIRAC
MUEAUS	1.00000	0.48347 <.0001	-0.02352 0.6967	0.86950 <.0001	-0.15273 0.0109	-0.00900 0.8815	0.10589 0.0785	0.68501 <.0001	-0.11121 0.0646	0.17637 0.0032	0.21784 0.0003	0.38711 <.0001	0.82494 <.0001	-0.15138 0.0117
MYRDIV	0.48347 <.0001	1.00000	0.01920 0.7504	0.49606 <.0001	0.00483 0.9362	0.12796 0.0333	0.14086 0.0190	0.41021 <.0001	-0.17863 0.0028	0.16286 0.0066	0.14114 0.0188	0.16288 0.0066	0.42609 <.0001	-0.26060 <.0001
NEOPED	-0.02352 0.6967	0.01920 0.7504	1.00000	0.02426 0.6877	0.28869 <.0001	0.37896 <.0001	-0.09686 0.1077	0.02062 0.7326	-0.13481 0.0248	-0.03112 0.6060	0.19078 0.0014	-0.12201 0.0425	-0.02799 0.6428	-0.18513 0.0020
NERVIL	0.86950 <.0001	0.49606 <.0001	0.02426 0.6877	1.00000	-0.07022 0.2441	-0.01870 0.7567	0.06560 0.2766	0.54692 <.0001	-0.03759 0.5333	0.14568 0.0152	0.38355 <.0001	0.34363 <.0001	0.90857 <.0001	-0.03652 0.5450
NOTFUS	-0.15273 0.0109	0.00483 0.9362	0.28869 <.0001	-0.07022 0.2441	1.00000	0.25396 <.0001	0.15775 0.0085	-0.02277 0.7060	0.07702 0.2013	-0.01066 0.8599	0.18127 0.0025	-0.18214 0.0023	-0.15930 0.0079	-0.05556 0.3569
NOTMEN	-0.00900 0.8815	0.12796 0.0333	0.37896 <.0001	-0.01870 0.7567	0.25396 <.0001	1.00000	0.01580 0.7934	0.13579 0.0238	-0.26304 <.0001	0.01615 0.7890	0.14096 0.0189	-0.09102 0.1307	-0.04482 0.4575	-0.36676 <.0001
PSECOL	0.10589 0.0785	0.14086 0.0190	-0.09686 0.1077	0.06560 0.2766	0.15775 0.0085	0.01580 0.7934	1.00000	0.12838 0.0327	-0.19389 0.0012	0.07461 0.2157	-0.09555 0.1126	0.02823 0.6399	0.03846 0.5239	-0.24077 <.0001
PSECRA	0.68501 <.0001	0.41021 <.0001	0.02062 0.7326	0.54692 <.0001	-0.02277 0.7060	0.13579 0.0238	0.12838 0.0327	1.00000	-0.13855 0.0211	0.23555 <.0001	0.11867 0.0485	0.47435 <.0001	0.49255 <.0001	-0.20050 0.0008
QUIACU	-0.11121 0.0646	-0.17863 0.0028	-0.13481 0.0248	-0.03759 0.5333	0.07702 0.2013	-0.26304 <.0001	-0.19389 0.0012	-0.13855 0.0211	1.00000	-0.08756 0.1461	0.03284 0.5863	0.00542 0.9284	-0.06181 0.3053	0.44563 <.0001
RAUANO	0.17637 0.0032	0.16286 0.0066	-0.03112 0.6060	0.14568 0.0152	-0.01066 0.8599	0.01615 0.7890	0.07461 0.2157	0.23555 <.0001	-0.08756 0.1461	1.00000	0.05367 0.3735	0.02719 0.6523	0.11221 0.0622	-0.14511 0.0156
RAUSIM	0.21784 0.0003	0.14114 0.0188	0.19078 0.0014	0.38355 <.0001	0.18127 0.0025	0.14096 0.0189	-0.09555 0.1126	0.11867 0.0485	0.03284 0.5863	0.05367 0.3735	1.00000	-0.01557 0.7965	0.26525 <.0001	0.18391 0.0021
RUBCIS	0.38711 <.0001	0.16288 0.0066	-0.12201 0.0425	0.34363 <.0001	-0.18214 0.0023	-0.09102 0.1307	0.02823 0.6399	0.47435 <.0001	0.00542 0.9284	0.02719 0.6523	-0.01557 0.7965	1.00000	0.30399 <.0001	0.04067 0.5002
UNCSPP	0.82494 <.0001	0.42609 <.0001	-0.02799 0.6428	0.90857 <.0001	-0.15930 0.0079	-0.04482 0.4575	0.03846 0.5239	0.49255 <.0001	-0.06181 0.3053	0.11221 0.0622	0.26525 <.0001	0.30399 <.0001	1.00000	-0.06883 0.2536
WEIRAC	-0.15138 0.0117	-0.26060 <.0001	-0.18513 0.0020	-0.03652 0.5450	-0.05556 0.3569	-0.36676 <.0001	-0.24077 <.0001	-0.20050 0.0008	0.44563 <.0001	-0.14511 0.0156	0.18391 0.0021	0.04067 0.5002	-0.06883 0.2536	1.00000

Appendix 5: Significance levels and parameters of models

Annual second order selection scale

Possum 48

R-Square 0.4190 Max-rescaled R-Square 0.7451

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	90.1450	6	<.0001
Score	68.1407	6	<.0001
Wald	18.9418	6	0.0043

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	7.6716	3.0219	6.4447	0.0111
LnPrefMean	1	-2.2365	0.6224	12.9138	0.0003
BLEFLU	1	-47.8866	17.9110	7.1481	0.0075
MYRDIV	1	19.2527	9.1702	4.4078	0.0358
QUIACU	1	-0.1094	0.0433	6.3921	0.0115
TierTOT	1	0.0475	0.0186	6.5392	0.0106
Ferns	1	-1.2803	0.3481	13.5256	0.0002

Possum 46

R-Square 0.3414 Max-rescaled R-Square 0.4636

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	69.3212	3	<.0001
Score	50.0052	3	<.0001
Wald	32.3841	3	<.0001

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	1.3133	0.2744	22.9121	<.0001
ASTFRA	1	124.1	34.4332	12.9880	0.0003
CYACOL	1	-31.8035	7.4973	17.9946	<.0001
PSECOL	1	-0.2907	0.0730	15.8476	<.0001

Possum44

R-Square 0.4913 Max-rescaled R-Square 0.8348

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	112.1981	7	<.0001
Score	76.0547	7	<.0001
Wald	17.2691	7	0.0157

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq

Intercept	1	15.6236	5.1005	9.3828	0.0022
NERVIL	1	-190.1	58.6013	10.5260	0.0012
PSECON	1	43.8047	14.5369	9.0802	0.0026
RAUSIM	1	-16.3436	6.1663	7.0251	0.0080
Tier1	1	0.0990	0.0481	4.2344	0.0396
Tier3	1	0.1257	0.0496	6.4146	0.0113
Shrub	1	-0.3390	0.1085	9.7581	0.0018
LnPrefMean	1	-3.9823	1.0349	14.8065	0.0001

Possum 42

R-Square 0.3902 Max-rescaled R-Square 0.5726

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	82.1093	3	<.0001
Score	71.2233	3	<.0001
Wald	34.1537	3	<.0001

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	-0.1729	0.8678	0.0397	0.8421
AGRCAP	1	-296.0	59.9713	24.3600	<.0001
NOTMEN	1	-0.1170	0.0223	27.5079	<.0001
SR	1	0.2776	0.0639	18.8857	<.0001

Possum 36

R-Square 0.2004 Max-rescaled R-Square 0.2864

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	37.1231	1	<.0001
Score	37.9517	1	<.0001
Wald	26.1721	1	<.0001

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	1.7495	0.2550	47.0840	<.0001
PSECOL	1	-0.3237	0.0633	26.1721	<.0001

Possum 34

R-Square 0.1756 Max-rescaled R-Square 0.3122

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	32.0463	2	<.0001
Score	41.3065	2	<.0001
Wald	17.1802	2	0.0002

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	-1.5433	1.3151	1.3770	0.2406
ARISER	1	-0.7853	0.1927	16.6077	<.0001
Sdi	1	3.8614	1.3850	7.7725	0.0053

Possum 30

R-Square 0.4178 Max-rescaled R-Square 0.6758

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	89.8036	3	<.0001
Score	70.6633	3	<.0001
Wald	26.5038	3	<.0001

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	7.5031	1.9013	15.5736	<.0001
RAUANO	1	-4.8744	1.4192	11.7962	0.0006
SR	1	-0.3629	0.0884	16.8561	<.0001
Tier3	1	0.0574	0.0243	5.5755	0.0182

Possum 28

R-Square 0.1139 Max-rescaled R-Square 0.1653

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	20.0733	1	<.0001
Score	12.6523	1	0.0004
Wald	11.8155	1	0.0006

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	-0.2423	0.3522	0.4731	0.4916
Shrub	1	0.1797	0.0523	11.8155	0.0006

Possum 24

R-Square 0.0762 Max-rescaled R-Square 0.1464

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	13.1642	1	0.0003
Score	19.3041	1	<.0001
Wald	9.3511	1	0.0022

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	2.3281	0.2821	68.1231	<.0001
BLEVUL	1	-21.4771	7.0233	9.3511	0.0022

Possum 22

R-Square 0.5055 Max-rescaled R-Square 0.8269

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	116.8983	7	<.0001
Score	74.6198	7	<.0001

Wald	16.4452	7	0.0213

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	13.8040	3.8694	12.7273	0.0004
BLEFLU	1	-76.1809	26.0796	8.5327	0.0035
BLEPRO	1	56.9167	24.7816	5.2750	0.0216
MYRDIV	1	34.7982	11.4462	9.2426	0.0024
NOTMEN	1	0.1859	0.0723	6.6135	0.0101
RAUSIM	1	-18.7837	6.3569	8.7312	0.0031
Ferns	1	-1.1927	0.3741	10.1611	0.0014
LnPrefMean	1	-2.0490	0.6071	11.3891	0.0007

Possum 20

R-Square 0.3659 Max-rescaled R-Square 0.5338

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	75.6137	5	<.0001
Score	56.5085	5	<.0001
Wald	30.2139	5	<.0001

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	10.2981	2.2606	20.7515	<.0001
CARSER	1	-1.8640	0.5782	10.3918	0.0013
NERVIL	1	-95.9435	37.0146	6.7187	0.0095
NERDEP	1	-42.2213	13.6707	9.5385	0.0020
Ferns	1	-0.6465	0.1669	15.0073	0.0001
PSECOL	1	-0.1472	0.0687	4.5870	0.0322

Possum 14

R-Square 0.3504 Max-rescaled R-Square 0.6131

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	71.6121	3	<.0001
Score	54.7316	3	<.0001
Wald	21.4599	3	<.0001

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	6.2343	1.5140	16.9570	<.0001
ASPBUL	1	-58.2811	18.3809	10.0536	0.0015
COPPAR	1	11.0679	3.9261	7.9470	0.0048
LnPrefAPR	1	-1.6754	0.4160	16.2193	<.0001

March/May second order selection scale

Possum 48

R-Square 0.3720 Max-rescaled R-Square 0.6855

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	77.2208	4	<.0001
Score	62.1047	4	<.0001
Wald	23.4012	4	0.0001

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	9.8306	2.3730	17.1621	<.0001
BLEFLU	1	-47.1466	16.0024	8.6802	0.0032
Tier3	1	0.0967	0.0403	5.7631	0.0164
Ferns	1	-0.7695	0.2206	12.1659	0.0005
LnPrefMean	1	-2.0040	0.4650	18.5750	<.0001

Possum 46

No significant result

Possum 44

R-Square 0.3427 Max-rescaled R-Square 0.6199

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	69.6481	4	<.0001
Score	52.1621	4	<.0001
Wald	21.0841	4	0.0003

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	4.7311	2.0806	5.1706	0.0230
BLEDIS	1	-1.2612	0.3384	13.8938	0.0002
Shrub	1	-0.1073	0.0434	6.1034	0.0135
LnPrefMean	1	-2.2953	0.5255	19.0752	<.0001
TierTOT	1	0.0546	0.0180	9.2066	0.0024

Possum 42

R-Square 0.4349 Max-rescaled R-Square 0.6651

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	94.7452	3	<.0001
Score	55.4793	3	<.0001
Wald	29.7264	3	<.0001

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	1.0915	0.8126	1.8045	0.1792
AGRCAP	1	-225.1	76.2982	8.7023	0.0032
NOTMEN	1	-0.0995	0.0240	17.1704	<.0001
Shrub	1	0.6506	0.1413	21.2145	<.0001

Possum 36

R-Square 0.1142 Max-rescaled R-Square 0.1733

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	20.1359	1	<.0001
Score	22.8576	1	<.0001
Wald	17.2793	1	<.0001

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	1.8450	0.2585	50.9328	<.0001
PSECOL	1	-0.2212	0.0532	17.2793	<.0001

Possum 34

R-Square	0.0632	Max-rescaled R-Square	0.1561

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	10.8398	1	0.0010
Score	14.3618	1	0.0002
Wald	11.2056	1	0.0008

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	3.4634	0.4916	49.6308	<.0001
CARSER	1	-1.3933	0.4162	11.2056	0.0008

Possum 30

R-Square	0.3767	Max-rescaled R-Square	0.6315

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	78.4695	2	<.0001
Score	78.7647	2	<.0001
Wald	23.6623	2	<.0001

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	3.0482	0.3879	61.7534	<.0001
COPROT	1	-2.7247	1.1289	5.8250	0.0158
RAUANO	1	-3.6946	0.9143	16.3274	<.0001

Possum 28

R-Square	0.0566	Max-rescaled R-Square	0.0853

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	9.6745	1	0.0019
Score	10.3103	1	0.0013
Wald	9.3788	1	0.0022

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	1.6367	0.2540	41.5182	<.0001
MYRDIV	1	-6.0319	1.9696	9.3788	0.0022

Possum 24

R-Square 0.0816 Max-rescaled R-Square 0.1644

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	14.1358	1	0.0002
Score	21.7725	1	<.0001
Wald	10.1245	1	0.0015

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	2.4882	0.3008	68.4221	<.0001
BLEVUL	1	-22.7497	7.1497	10.1245	0.0015

Possum 22

R-Square 0.5148 Max-rescaled R-Square 0.8420

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	120.0341	7	<.0001
Score	73.6175	7	<.0001
Wald	18.1309	7	0.0114

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	16.7338	4.5590	13.4726	0.0002
BLEFLU	1	-93.8247	28.4971	10.8401	0.0010
BLEDIS	1	-1.3081	0.3728	12.3153	0.0004
NOTMEN	1	0.2364	0.0770	9.4171	0.0021
MYRDIV	1	23.0725	7.4753	9.5264	0.0020
RAUSIM	1	-15.3794	6.0338	6.4967	0.0108
LnPrefMean	1	-3.7096	1.1114	11.1406	0.0008
WEIRAC	1	0.1234	0.0501	6.0606	0.0138

Possum 20

R-Square 0.2436 Max-rescaled R-Square 0.3860

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	46.3540	4	<.0001
Score	38.1155	4	<.0001
Wald	24.0764	4	<.0001

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	8.1185	2.0020	16.4450	<.0001

BLEDIS	1	-0.3571	0.1465	5.9419	0.0148
CARSER	1	-1.8578	0.4376	18.0253	<.0001
NERDEP	1	-35.6735	12.5090	8.1329	0.0043
NERVIL	1	-88.1327	37.7306	5.4562	0.0195

Possum 14

R-Square 0.3504 Max-rescaled R-Square 0.6131

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	71.6121	3	<.0001
Score	54.7316	3	<.0001
Wald	21.4599	3	<.0001

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	6.2343	1.5140	16.9570	<.0001
ASPBUL	1	-58.2811	18.3809	10.0536	0.0015
COPPAR	1	11.0679	3.9261	7.9470	0.0048
LnPrefAPR	1	-1.6754	0.4160	16.2193	<.0001

July/September second order selection scale

Possum 48

R-Square 0.2717 Max-rescaled R-Square 0.5973

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	52.6302	3	<.0001
Score	64.5577	3	<.0001
Wald	20.7237	3	0.0001

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	3.7919	0.6619	32.8176	<.0001
CARSER	1	-1.6164	0.5326	9.2104	0.0024
MYRDIV	1	41.0910	14.4692	8.0651	0.0045
CYASMI	1	-3.8345	0.9410	16.6040	<.0001

Possum 46

R-Square 0.1538 Max-rescaled R-Square 0.2488

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	27.7224	2	<.0001
Score	32.3071	2	<.0001
Wald	20.4835	2	<.0001

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Error	Chi-Square	Pr > ChiSq
Intercept	1	2.4885	0.3324	56.0553	<.0001
CYACOL	1	-14.9405	5.0011	8.9248	0.0028
PSECOL	1	-0.1930	0.0550	12.3136	0.0004

Possum 44

R-Square 0.1761 Max-rescaled R-Square 0.3641

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	32.1485	3	<.0001
Score	41.6216	3	<.0001
Wald	24.7905	3	<.0001

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	3.7438	0.5355	48.8713	<.0001
WEIRAC	1	-0.0578	0.0187	9.5333	0.0020
QUIACU	1	-0.0652	0.0271	5.7971	0.0161
CYASMI	1	-0.9507	0.3905	5.9267	0.0149

Possum 42

R-Square 0.3154 Max-rescaled R-Square 0.5221

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	62.8954	4	<.0001
Score	54.9033	4	<.0001
Wald	30.9423	4	<.0001

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	4.1994	0.6951	36.5026	<.0001
NOTMEN	1	-0.0847	0.0194	19.1077	<.0001
NEOPED	1	-0.4028	0.1637	6.0546	0.0139
RAUANO	1	10.3618	4.4090	5.5232	0.0188
FUCEXC	1	-5.7601	1.7092	11.3580	0.0008

Possum 36

R-Square 0.3306 Max-rescaled R-Square 0.4945

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	66.6391	4	<.0001
Score	63.5247	4	<.0001
Wald	36.5365	4	<.0001

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	3.3014	0.4916	45.1026	<.0001
GRILIT	1	-0.7942	0.3197	6.1715	0.0130
LEPSUP	1	-28.3840	9.4493	9.0229	0.0027
MICAVE	1	1.2216	0.4750	6.6151	0.0101
PSECOL	1	-0.4452	0.0833	28.5691	<.0001

Possum 34

R-Square 0.1788 Max-rescaled R-Square 0.3432

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	32.6923	2	<.0001
Score	41.0634	2	<.0001
Wald	24.4295	2	<.0001

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	0.1431	1.2607	0.0129	0.9096
Sdi	1	3.4687	1.4177	5.9861	0.0144
LnPrefCondit	1	-1.8314	0.3792	23.3258	<.0001

Possum 30

R-Square 0.3056 Max-rescaled R-Square 0.5632

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	60.5519	3	<.0001
Score	67.5495	3	<.0001
Wald	20.6839	3	0.0001

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	8.1756	1.9163	18.2018	<.0001
RAUANO	1	-2.0787	0.6604	9.9066	0.0016
SR	1	-0.3182	0.0937	11.5238	0.0007
CARSER	1	2.0376	0.8995	5.1315	0.0235

Possum 28

R-Square 0.0612 Max-rescaled R-Square 0.0990

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	10.4812	1	0.0012
Score	9.7776	1	0.0018
Wald	9.1841	1	0.0024

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Error	Chi-Square	Pr > ChiSq
Intercept	1	-1.8805	1.0851	3.0033	0.0831
sdi	1	3.3144	1.0937	9.1841	0.0024

Possum 24

R-Square 0.3122 Max-rescaled R-Square 0.6649

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	62.1343	6	<.0001
Score	58.0297	6	<.0001
Wald	19.9662	6	0.0028

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	-1.9643	1.8704	1.1029	0.2936
AGRCAP	1	-378.1	126.2	8.9822	0.0027
ASTFRA	1	-109.3	42.5795	6.5856	0.0103
NERVIL	1	-75.8722	36.7105	4.2715	0.0388
SR	1	0.7456	0.2011	13.7425	0.0002
FUCEXC	1	-12.9849	4.8653	7.1230	0.0076
NOTMEN	1	-0.0520	0.0238	4.7798	0.0288

Possum 22

R-Square 0.2451 Max-rescaled R-Square 0.4814

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	46.6701	2	<.0001
Score	40.5147	2	<.0001
Wald	20.2336	2	<.0001

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	7.9044	1.5298	26.6966	<.0001
LnPrefMean	1	-1.7171	0.3846	19.9319	<.0001
CARSER	1	-1.1119	0.4936	5.0746	0.0243

Possum 20

R-Square 0.3293 Max-rescaled R-Square 0.5761

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	66.2943	4	<.0001
Score	66.0833	4	<.0001
Wald	22.9647	4	0.0001

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	4.3165	0.9112	22.4407	<.0001
CARSER	1	-1.3327	0.5166	6.6557	0.0099
CYASMI	1	-4.8205	1.1140	18.7233	<.0001
MYRDIV	1	15.3447	6.4057	5.7383	0.0166
RAUSIM	1	-12.0760	4.4671	7.3080	0.0069

November/January second order selection scale

Possum 48

R-Square 0.3893 Max-rescaled R-Square 0.7318

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	81.8698	6	<.0001
Score	59.3540	6	<.0001
Wald	16.9485	6	0.0095

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	7.0009	2.7517	6.4733	0.0110
Tier3	1	0.1416	0.0514	7.5875	0.0059
Tier4	1	0.2158	0.1032	4.3710	0.0366
LnPrefMean	1	-1.8214	0.5404	11.3598	0.0008
Shrub	1	-0.1290	0.0472	7.4862	0.0062
Ferns	1	-2.5825	0.9525	7.3506	0.0067
CARSER	1	-1.7090	0.8086	4.4667	0.0346

Possum46

R-Square 0.2077 Max-rescaled R-Square 0.2943

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	38.6563	1	<.0001
Score	38.7585	1	<.0001
Wald	26.8103	1	<.0001

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	1.6991	0.2515	45.6317	<.0001
PSECOL	1	-0.3337	0.0644	26.8103	<.0001

Possum 44

R-Square 0.3541 Max-rescaled R-Square 0.7129

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	72.5555	5	<.0001
Score	53.6422	5	<.0001

Wald	15.0548	5	0.0101

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	19.5281	5.2545	13.8120	0.0002
NEOPED	1	1.9380	0.7029	7.6013	0.0058
NERVIL	1	-144.4	44.4995	10.5295	0.0012
QUIACU	1	-0.2429	0.0750	10.4795	0.0012
RAUSIM	1	-12.8786	5.3709	5.7497	0.0165
LnPrefMean	1	-2.8305	0.9109	9.6559	0.0019

Possum 36

R-Square 0.3074 Max-rescaled R-Square 0.4920

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	60.9735	2	<.0001
Score	62.6600	2	<.0001
Wald	32.0397	2	<.0001

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	3.8381	0.5594	47.0759	<.0001
GRILIT	1	-1.2484	0.3391	13.5540	0.0002
PSECOL	1	-0.3843	0.0786	23.9227	<.0001

Possum 34

R-Square 0.2551 Max-rescaled R-Square 0.5433

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	48.8936	3	<.0001
Score	25.8645	3	<.0001
Wald	18.2720	3	0.0004

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	0.4430	0.7659	0.3346	0.5629
ASTFRA	1	-89.0974	25.9223	11.8136	0.0006
MEUAUS2	1	-0.8666	0.3721	5.4224	0.0199
Shrub	1	0.9098	0.2371	14.7204	0.0001

Possum 28

R-Square 0.1589 Max-rescaled R-Square 0.2543

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	28.7300	3	<.0001
Score	28.3068	3	<.0001
Wald	22.3560	3	<.0001

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	-1.5226	1.1397	1.7847	0.1816
MYRDIV	1	-8.2334	2.2834	13.0017	0.0003
Sdi	1	3.8687	1.1878	10.6085	0.0011
ARISER	1	-0.4443	0.1253	12.5618	0.0004

Possum 24

R-Square 0.1088 Max-rescaled R-Square 0.2820

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	19.1299	2	<.0001
Score	33.9876	2	<.0001
Wald	16.2857	2	0.0003

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	3.7373	0.5151	52.6347	<.0001
FUCEXC	1	-5.3005	1.5568	11.5923	0.0007
NEOPED	1	-0.4946	0.1592	9.6500	0.0019

Possum 22

R-Square 0.2278 Max-rescaled R-Square 0.4711

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	42.9076	2	<.0001
Score	36.9879	2	<.0001
Wald	18.9527	2	<.0001

Analysis of Maximum Likelihood Estimates

Parameter	DF	Estimate	Standard Error	Chi-Square	Pr > ChiSq
Intercept	1	9.1702	1.9154	22.9210	<.0001
LnPrefMean	1	-1.6946	0.4025	17.7216	<.0001
Ferns	1	-0.3096	0.1434	4.6610	0.0309

Annual third order selection scale

Possum 48

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	3	120.04950	40.01650	13.75	<.0001
Error	20	58.18959	2.90948		
Corrected Total	23	178.23910			

Root MSE	1.70572	R-Square	0.6735
Dependent Mean	6.47958	Adj R-Sq	0.6246
Coeff Var	26.32453		

Parameter Estimates

Parameter	Standard

Variable	DF	Estimate	Error	t Value	Pr > |t|
Intercept	1	8.43590	0.47077	17.92	<.0001
QUIACU	1	-0.15616	0.02849	-5.48	<.0001
BLENOV	1	-13.13310	5.09289	-2.58	0.0179
BLEVUL	1	-38.16776	14.84043	-2.57	0.0182

Possum 46

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	3	120.04950	40.01650	13.75	<.0001
Error	20	58.18959	2.90948		
Corrected Total	23	178.23910			

Root MSE	1.70572	R-Square	0.6735
Dependent Mean	6.47958	Adj R-Sq	0.6246
Coeff Var	26.32453		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	8.43590	0.47077	17.92	<.0001
QUIACU	1	-0.15616	0.02849	-5.48	<.0001
BLENOV	1	-13.13310	5.09289	-2.58	0.0179
BLEVUL	1	-38.16776	14.84043	-2.57	0.0182

Possum 44

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	19.64305	19.64305	8.15	0.0058
Error	62	149.34255	2.40875		
Corrected Total	63	168.98560			

Root MSE	1.55202	R-Square	0.1162
Dependent Mean	7.72791	Adj R-Sq	0.1020
Coeff Var	20.08326		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	8.30257	0.27952	29.70	<.0001
LnPrefCondit	1	-0.82837	0.29008	-2.86	0.0058

Possum 42

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	5	156.15407	31.23081	11.38	<.0001
Error	21	57.64414	2.74496		
Corrected Total	26	213.79821			

Root MSE	1.65679	R-Square	0.7304
Dependent Mean	5.99094	Adj R-Sq	0.6662
Coeff Var	27.65497		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	10.32905	1.96228	5.26	<.0001
NOTFUS	1	-0.06765	0.02731	-2.48	0.0218

BLEPRO	1	-92.58773	19.95642	-4.64	0.0001
ASTFRA	1	125.84418	37.05070	3.40	0.0027
NEOPED	1	-0.91530	0.31078	-2.95	0.0077
NERVIL	1	53.25078	22.44221	2.37	0.0273

Possum 36

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	18.05456	18.05456	6.82	0.0125
Error	41	108.50786	2.64653		
Corrected Total	42	126.56242			

Root MSE	1.62682	R-Square	0.1427
Dependent Mean	7.94736	Adj R-Sq	0.1217
Coeff Var	20.46991		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	8.49917	0.32586	26.08	<.0001
COPRHA	1	-5.38292	2.06093	-2.61	0.0125

Possum 34

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	36.23598	36.23598	10.45	0.0023
Error	46	159.47902	3.46694		
Corrected Total	47	195.71500			

Root MSE	1.86197	R-Square	0.1851
Dependent Mean	7.37565	Adj R-Sq	0.1674
Coeff Var	25.24483		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	8.31651	0.39613	20.99	<.0001
LnPrefDEC	1	-0.76746	0.23739	-3.23	0.0023

Possum 34

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	35.28365	35.28365	7.71	0.0110
Error	22	100.69815	4.57719		
Corrected Total	23	135.98180			

Root MSE	2.13944	R-Square	0.2595
Dependent Mean	7.10365	Adj R-Sq	0.2258
Coeff Var	30.11744		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	5.01296	0.87048	5.76	<.0001
LnPrefAUG	1	1.05335	0.37939	2.78	0.0110

Possum 30

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	4	68.98548	17.24637	13.51	<.0001
Error	26	33.18514	1.27635		
Corrected Total	30	102.17063			

Root MSE	1.12976	R-Square	0.6752
Dependent Mean	7.85126	Adj R-Sq	0.6252
Coeff Var	14.38950		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	8.04950	1.57054	5.13	<.0001
HerbGrass	1	0.87744	0.24524	3.58	0.0014
COPFOE	1	13.43362	2.68983	4.99	<.0001
PSECRA	1	1.96574	0.55641	3.53	0.0016
TierTOT	1	-0.01933	0.00727	-2.66	0.0133

Possum 28

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	4	66.75504	16.68876	9.24	<.0001
Error	40	72.22575	1.80564		
Corrected Total	44	138.98079			

Root MSE	1.34374	R-Square	0.4803
Dependent Mean	7.85096	Adj R-Sq	0.4284
Coeff Var	17.11565		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	6.28048	0.70493	8.91	<.0001
NEOPED	1	-1.03775	0.23170	-4.48	<.0001
Ferns	1	0.39213	0.10272	3.82	0.0005
RAUANO	1	-8.82440	2.68976	-3.28	0.0022
LnPrefAUG	1	0.46345	0.18371	2.52	0.0157

Possum 24

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	67.76634	33.88317	6.27	0.0091
Error	17	91.85073	5.40298		
Corrected Total	19	159.61707			

Root MSE	2.32443	R-Square	0.4246
Dependent Mean	6.90787	Adj R-Sq	0.3569
Coeff Var	33.64906		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	11.83952	1.54572	7.66	<.0001
Tier4	1	-0.11319	0.03561	-3.18	0.0055
HOLLAN	1	-7.20561	3.14026	-2.29	0.0348

Possum 22

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F

Model	3	68.89255	22.96418	7.43	0.0009
Error	26	80.34915	3.09035		
Corrected Total	29	149.24170			

Root MSE	1.75794	R-Square	0.4616
Dependent Mean	6.96509	Adj R-Sq	0.3995
Coeff Var	25.23930		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	8.98786	1.87519	4.79	<.0001
NOTMEN	1	0.13596	0.04711	2.89	0.0078
Tier2	1	-0.10622	0.03370	-3.15	0.0041
WEIRAC	1	0.10892	0.03010	3.62	0.0013

Possum 20

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	4	65.93635	16.48409	7.63	0.0001
Error	39	84.23873	2.15997		
Corrected Total	43	150.17508			

Root MSE	1.46968	R-Square	0.4391
Dependent Mean	6.93908	Adj R-Sq	0.3815
Coeff Var	21.17978		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	2.65951	2.33482	1.14	0.2616
NEOPED	1	1.24919	0.28603	4.37	<.0001
SR	1	0.23105	0.06567	3.52	0.0011
COVER	1	-0.04587	0.02154	-2.13	0.0396
BLEDIS	1	0.42013	0.15464	2.72	0.0098

Possum 14

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	4	40.00723	10.00181	6.15	0.0022
Error	20	32.54942	1.62747		
Corrected Total	24	72.55666			

Root MSE	1.27572	R-Square	0.5514
Dependent Mean	7.75008	Adj R-Sq	0.4617
Coeff Var	16.46079		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	12.22463	1.49885	8.16	<.0001
METUMB	1	-10.96914	3.48582	-3.15	0.0051
NEOPED	1	-0.68160	0.23317	-2.92	0.0084
BLEPRO	1	-30.68456	14.11829	-2.17	0.0419
Tier2	1	-0.06280	0.02461	-2.55	0.0190

March/May third order selection scale

Possum 48

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F

Model	5	43.43293	8.68659	8.68	0.0004
Error	16	16.00417	1.00026		
Corrected Total	21	59.43710			

Root MSE	1.00013	R-Square	0.7307
Dependent Mean	7.49393	Adj R-Sq	0.6466
Coeff Var	13.34588		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	-2.06318	2.15488	-0.96	0.3526
PSECOL	1	0.39533	0.08642	4.57	0.0003
COVER	1	0.05728	0.02201	2.60	0.0193
CARSER	1	1.15271	0.42216	2.73	0.0148
NEOPED	1	-1.15115	0.40935	-2.81	0.0125
LnPrefAPR	1	1.44365	0.40840	3.53	0.0028

Possum 46

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	6	43.47365	7.24561	6.74	0.0003
Error	24	25.81821	1.07576		
Corrected Total	30	69.29186			

Root MSE	1.03719	R-Square	0.6274
Dependent Mean	7.68605	Adj R-Sq	0.5342
Coeff Var	13.49441		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	5.42663	0.91088	5.96	<.0001
PSECON	1	-10.48016	3.98945	-2.63	0.0148
CARSER	1	1.68750	0.41326	4.08	0.0004
COPPAR	1	1.65630	0.55449	2.99	0.0064
CYACOL	1	-13.34729	3.77374	-3.54	0.0017
NOTFUS	1	0.02655	0.01037	2.56	0.0171
Vines	1	-1.79329	0.62724	-2.86	0.0087

Possum 44

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	26.08939	26.08939	12.00	0.0023
Error	21	45.65223	2.17392		
Corrected Total	22	71.74162			

Root MSE	1.47442	R-Square	0.3637
Dependent Mean	7.51213	Adj R-Sq	0.3334
Coeff Var	19.62719		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	5.32898	0.70119	7.60	<.0001
PrefAPR	1	0.08921	0.02575	3.46	0.0023

Possum 42

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F

Model	2	16.50608	8.25304	4.13	0.0248
Error	34	67.97072	1.99914		
Corrected Total	36	84.47679			

Root MSE	1.41391	R-Square	0.1954
Dependent Mean	7.91217	Adj R-Sq	0.1481
Coeff Var	17.87006		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	9.70036	0.71565	13.55	<.0001
NOTFUS	1	-0.02188	0.00870	-2.52	0.0167
NERDEP	1	-32.84350	14.80859	-2.22	0.0333

Possum 36

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	4	54.79761	13.69940	7.76	0.0002
Error	33	58.26272	1.76554		
Corrected Total	37	113.06033			

Root MSE	1.32874	R-Square	0.4847
Dependent Mean	7.78367	Adj R-Sq	0.4222
Coeff Var	17.07080		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	5.36620	1.54729	3.47	0.0015
TierTOT	1	0.02536	0.00806	3.14	0.0035
FUCEXC	1	-11.19179	3.73805	-2.99	0.0052
LnPrefDEC	1	-0.75132	0.21944	-3.42	0.0017
Tier4	1	-0.03188	0.01512	-2.11	0.0427

Possum 34

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	3	24.15296	8.05099	29.97	0.0001
Error	8	2.14936	0.26867		
Corrected Total	11	26.30232			

Root MSE	0.51833	R-Square	0.9183
Dependent Mean	8.09171	Adj R-Sq	0.8876
Coeff Var	6.40574		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	9.66383	0.34589	27.94	<.0001
NERVIL	1	-81.63044	9.24862	-8.83	<.0001
BLEFLU	1	37.18293	8.61001	4.32	0.0026
PSECON	1	7.08728	2.36078	3.00	0.0170

Possum 30

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	36.06906	18.03453	8.95	0.0012
Error	25	50.36736	2.01469		
Corrected Total	27	86.43642			

Root MSE	1.41940	R-Square	0.4173
Dependent Mean	7.74020	Adj R-Sq	0.3707
Coeff Var	18.33802		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	9.96203	0.59061	16.87	<.0001
Ferns	1	-0.70861	0.17021	-4.16	0.0003
COPROT	1	-0.39214	0.15788	-2.48	0.0201

Possum 28

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	12	73.93059	6.16088	14.40	<.0001
Error	26	11.12428	0.42786		
Corrected Total	38	85.05487			

Root MSE	0.65411	R-Square	0.8692
Dependent Mean	7.76035	Adj R-Sq	0.8088
Coeff Var	8.42884		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	6.40859	0.66643	9.62	<.0001
Shrub	1	-0.21696	0.03702	-5.86	<.0001
COPRHA	1	3.75153	1.25767	2.98	0.0061
TierTOT	1	0.01552	0.00252	6.16	<.0001
AGRCAP	1	101.36331	26.41396	3.84	0.0007
GRILIT	1	-0.42676	0.19690	-2.17	0.0395
CYASMI	1	-9.91809	3.49183	-2.84	0.0086
BLEPRO	1	9.51830	3.59009	2.65	0.0135
CARSER	1	0.87173	0.23437	3.72	0.0010
PNEPEN	1	-33.30074	10.12945	-3.29	0.0029
RAUANO	1	-4.29956	1.79318	-2.40	0.0240
LEPSUP	1	20.39526	7.25985	2.81	0.0093
SR	1	-0.07737	0.03583	-2.16	0.0402

Possum 24

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	3	38.35874	12.78625	9.23	0.0013
Error	14	19.39202	1.38514		
Corrected Total	17	57.75075			

Root MSE	1.17692	R-Square	0.6642
Dependent Mean	7.96216	Adj R-Sq	0.5923
Coeff Var	14.78144		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	11.76202	0.89882	13.09	<.0001
COPFOE	1	-12.91975	3.76114	-3.44	0.0040
NOTFUS	1	-0.03782	0.01164	-3.25	0.0058
AGRCAP	1	-124.15990	44.81292	-2.77	0.0150

Possum 22

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F

Model	7	50.61047	7.23007	10.11	<.0001
Error	22	15.72692	0.71486		
Corrected Total	29	66.33739			

Root MSE	0.84549	R-Square	0.7629
Dependent Mean	8.18817	Adj R-Sq	0.6875
Coeff Var	10.32580		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	4.45660	0.81060	5.50	<.0001
CYACOL	1	-39.89620	13.51919	-2.95	0.0074
CARSER	1	0.78560	0.28149	2.79	0.0107
BLEPRO	1	-22.65581	9.74219	-2.33	0.0297
PrefAPR	1	0.03993	0.01600	2.50	0.0206
METUMB	1	-9.36037	2.36776	-3.95	0.0007
BLEFLU	1	-26.20931	11.42877	-2.29	0.0318
SR	1	0.22885	0.05655	4.05	0.0005

Possum 20

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	5	57.43854	11.48771	8.65	<.0001
Error	27	35.87210	1.32860		
Corrected Total	32	93.31065			

Root MSE	1.15265	R-Square	0.6156
Dependent Mean	7.46065	Adj R-Sq	0.5444
Coeff Var	15.44969		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	5.97544	0.43755	13.66	<.0001
LnPrefAPR	1	0.77694	0.16333	4.76	<.0001
BLECOL	1	-51.61403	16.42330	-3.14	0.0040
URTINC	1	127.55601	30.00160	4.25	0.0002
HYPRUF	1	-75.26999	22.79938	-3.30	0.0027
MUEAUS	1	5.36921	2.49055	2.16	0.0402

Possum 14

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	5	52.40168	10.48034	10.68	<.0001
Error	19	18.64537	0.98134		
Corrected Total	24	71.04705			

Root MSE	0.99062	R-Square	0.7376
Dependent Mean	7.75592	Adj R-Sq	0.6685
Coeff Var	12.77249		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	10.55636	1.24349	8.49	<.0001
METUMB	1	-14.93787	2.92899	-5.10	<.0001
LnPrefCondit	1	2.31831	0.62276	3.72	0.0014
NEOPED	1	-0.77414	0.18307	-4.23	0.0005
BLEPRO	1	-36.50034	11.10825	-3.29	0.0039
Tier2	1	-0.04744	0.01952	-2.43	0.0252

July/September second order selection scale

Possum 48

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	5	27.04462	5.40892	5.78	0.0116
Error	9	8.41792	0.93532		
Corrected Total	14	35.46255			

Root MSE	0.96712	R-Square	0.7626
Dependent Mean	7.75345	Adj R-Sq	0.6308
Coeff Var	12.47343		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	3.65314	1.55714	2.35	0.0436
SR	1	0.16900	0.06956	2.43	0.0380
BLEVUL	1	-79.91662	22.14660	-3.61	0.0057
WEIRAC	1	0.14087	0.03735	3.77	0.0044
CYASMI	1	-0.68630	0.26520	-2.59	0.0293
QUIACU	1	-0.49518	0.15381	-3.22	0.0105

Possum 46

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	15.77046	15.77046	7.70	0.0096
Error	29	59.41076	2.04865		
Corrected Total	30	75.18122			

Root MSE	1.43131	R-Square	0.2098
Dependent Mean	7.46384	Adj R-Sq	0.1825
Coeff Var	19.17659		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	5.11560	0.88454	5.78	<.0001
NERVIL	1	53.22464	19.18334	2.77	0.0096

Possum 44

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	4	53.53162	13.38290	7.65	0.0027
Error	12	20.99565	1.74964		
Corrected Total	16	74.52727			

Root MSE	1.32274	R-Square	0.7183
Dependent Mean	7.18400	Adj R-Sq	0.6244
Coeff Var	18.41230		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	13.20776	2.21368	5.97	<.0001
NOTFUS	1	-0.10823	0.02787	-3.88	0.0022
NOTMEN	1	0.23953	0.05575	4.30	0.0010
ASTFRA	1	107.03858	31.41996	3.41	0.0052
BLEFLU	1	-37.59152	17.13418	-2.19	0.0487

Possum 42

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	19.42679	9.71340	4.92	0.0154
Error	26	51.31972	1.97384		
Corrected Total	28	70.74652			

Root MSE	1.40493	R-Square	0.2746
Dependent Mean	8.13865	Adj R-Sq	0.2188
Coeff Var	17.26248		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	7.76364	0.74031	10.49	<.0001
COPPAR	1	10.08493	3.70374	2.72	0.0114
Shrub	1	-0.30051	0.14083	-2.13	0.0425

Possum 36

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	5	68.20917	13.64183	9.00	<.0001
Error	34	51.54666	1.51608		
Corrected Total	39	119.75584			

Root MSE	1.23129	R-Square	0.5696
Dependent Mean	7.24163	Adj R-Sq	0.5063
Coeff Var	17.00297		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	7.27002	0.47842	15.20	<.0001
HOLLAN	1	-12.68565	3.17609	-3.99	0.0003
PSECOL	1	0.18821	0.05096	3.69	0.0008
ASTFRA	1	-127.39205	30.13598	-4.23	0.0002
POLVES	1	35.16429	10.98380	3.20	0.0030
COPPAR	1	-7.44399	2.48686	-2.99	0.0051

Possum 34

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	4	61.46674	15.36669	11.19	0.0002
Error	15	20.60230	1.37349		
Corrected Total	19	82.06904			

Root MSE	1.17196	R-Square	0.7490
Dependent Mean	6.97720	Adj R-Sq	0.6820
Coeff Var	16.79698		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	8.47503	0.73727	11.50	<.0001
LEPSUP	1	-48.52194	14.25703	-3.40	0.0039
DICSQU	1	-7.78895	2.17541	-3.58	0.0027
NOTFUS	1	-0.02222	0.00930	-2.39	0.0304
COPRHA	1	5.05086	2.28845	2.21	0.0433

Possum 30

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	5	43.37007	8.67401	12.41	<.0001
Error	16	11.18374	0.69898		
Corrected Total	21	54.55380			

Root MSE	0.83605	R-Square	0.7950
Dependent Mean	8.10251	Adj R-Sq	0.7309
Coeff Var	10.31843		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	17.12318	2.16623	7.90	<.0001
PSECRA	1	2.19302	0.48211	4.55	0.0003
Tier4	1	-0.08997	0.02521	-3.57	0.0026
Tier1	1	-0.09087	0.01813	-5.01	0.0001
COPFOE	1	8.66913	2.50155	3.47	0.0032
LnPrefAUG	1	-1.38042	0.52093	-2.65	0.0175

Possum 28

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	4	71.37453	17.84363	18.51	<.0001
Error	26	25.06095	0.96388		
Corrected Total	30	96.43548			

Root MSE	0.98178	R-Square	0.7401
Dependent Mean	7.80002	Adj R-Sq	0.7001
Coeff Var	12.58682		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	2.77307	0.69128	4.01	0.0005
Ferns	1	0.53903	0.10238	5.26	<.0001
MYRDIV	1	8.86352	2.04513	4.33	0.0002
COPRHA	1	5.95240	1.70675	3.49	0.0018
BLEPRO	1	11.81127	5.09325	2.32	0.0285

Possum 24

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	16.74108	16.74108	8.29	0.0121
Error	14	28.25958	2.01854		
Corrected Total	15	45.00067			

Root MSE	1.42075	R-Square	0.3720
Dependent Mean	7.92260	Adj R-Sq	0.3272
Coeff Var	17.93293		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	9.87045	0.76396	12.92	<.0001
Ferns	1	-0.59515	0.20666	-2.88	0.0121

Possum 22

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	22.20575	22.20575	7.39	0.0146
Error	17	51.10829	3.00637		
Corrected Total	18	73.31404			

Root MSE	1.73389	R-Square	0.3029
Dependent Mean	7.43210	Adj R-Sq	0.2619
Coeff Var	23.32972		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	6.80680	0.45953	14.81	<.0001
COPFOE	1	17.89279	6.58365	2.72	0.0146

Possum 20

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	6	60.09280	10.01547	33.35	<.0001
Error	18	5.40530	0.30029		
Corrected Total	24	65.49810			

Root MSE	0.54799	R-Square	0.9175
Dependent Mean	7.59578	Adj R-Sq	0.8900
Coeff Var	7.21442		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	-3.76542	0.87866	-4.29	0.0004
LnPrefMean	1	1.52235	0.14058	10.83	<.0001
SR	1	0.10702	0.04597	2.33	0.0318
COPRHA	1	18.43688	2.85952	6.45	<.0001
CYASMI	1	-0.83059	0.13471	-6.17	<.0001
CYACOL	1	24.71735	6.38188	3.87	0.0011
BLEFLU	1	36.49535	11.17192	3.27	0.0043

November/January third order selection

Possum 48

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	14.86537	14.86537	5.08	0.0362
Error	19	55.58700	2.92563		
Corrected Total	20	70.45237			

Root MSE	1.71045	R-Square	0.2110
Dependent Mean	7.42916	Adj R-Sq	0.1695
Coeff Var	23.02344		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	7.86780	0.42093	18.69	<.0001
QUIACU	1	-0.07111	0.03154	-2.25	0.0362

Possum 46

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	5	47.51604	9.50321	6.24	0.0002
Error	44	67.01205	1.52300		
Corrected Total	49	114.52809			

Root MSE	1.23410	R-Square	0.4149
Dependent Mean	7.60808	Adj R-Sq	0.3484
Coeff Var	16.22091		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	6.97678	0.71681	9.73	<.0001
PRUFER	1	-6.64868	2.38180	-2.79	0.0077
CYASMI	1	1.21326	0.41630	2.91	0.0056
COPRHA	1	8.92656	2.66884	3.34	0.0017
QUIACU	1	0.11189	0.03451	3.24	0.0023
Tier2	1	-0.02976	0.01327	-2.24	0.0300

Possum 44

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	6	76.20300	12.70050	29.88	<.0001
Error	11	4.67563	0.42506		
Corrected Total	17	80.87863			

Root MSE	0.65196	R-Square	0.9422
Dependent Mean	7.17432	Adj R-Sq	0.9107
Coeff Var	9.08746		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	-6.64381	1.24985	-5.32	0.0002
NOTMEN	1	0.24620	0.02855	8.62	<.0001
WEIRAC	1	0.21852	0.02228	9.81	<.0001
BLECOL	1	86.14859	11.79979	7.30	<.0001
QUIACU	1	0.15214	0.02089	7.28	<.0001
COPRHA	1	18.72161	3.43427	5.45	0.0002
METUMB	1	4.99752	1.83496	2.72	0.0198

Possum 36

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	3	35.71093	11.90364	5.71	0.0035
Error	28	58.39796	2.08564		
Corrected Total	31	94.10889			

Root MSE	1.44418	R-Square	0.3795
Dependent Mean	7.47869	Adj R-Sq	0.3130
Coeff Var	19.31054		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	7.92395	0.55212	14.35	<.0001
MYRDIV	1	-7.34952	3.53540	-2.08	0.0469
PSECRA	1	2.19925	0.95869	2.29	0.0295
LnPrefDEC	1	-1.12506	0.32689	-3.44	0.0018

Possum 34

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	3	37.61133	12.53711	13.08	0.0004
Error	12	11.50287	0.95857		
Corrected Total	15	49.11420			

Root MSE	0.97907	R-Square	0.7658
Dependent Mean	7.46821	Adj R-Sq	0.7072
Coeff Var	13.10980		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	6.24242	0.38261	16.32	<.0001
BLECOL	1	-114.30707	22.80797	-5.01	0.0003
SCHDIG	1	13.47702	4.60508	2.93	0.0127
LnPrefDEC	1	0.51699	0.14966	3.45	0.0048

Possum 28

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	9	50.31953	5.59106	10.56	<.0001
Error	22	11.64880	0.52949		
Corrected Total	31	61.96833			

Root MSE	0.72766	R-Square	0.8120
Dependent Mean	7.55033	Adj R-Sq	0.7351
Coeff Var	9.63747		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	8.60166	0.42615	20.18	<.0001
FUCEXC	1	7.01805	1.33767	5.25	<.0001
PrefDEC	1	-0.04822	0.01892	-2.55	0.0183
Vines	1	-1.89955	0.67331	-2.82	0.0099
RAUSIM	1	-9.19137	1.70943	-5.38	<.0001
BLEPRO	1	9.61263	4.03483	2.38	0.0263
ELAHOO	1	-12.07216	4.27108	-2.83	0.0098
COPFOE	1	-4.93611	1.87900	-2.63	0.0154
UNCSPP	1	-7.30059	1.57426	-4.64	0.0001
NOTMEN	1	0.03150	0.01266	2.49	0.0209

Possum 24

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	32.27305	16.13653	9.66	0.0074
Error	8	13.36628	1.67079		
Corrected Total	10	45.63934			

Root MSE	1.29259	R-Square	0.7071
Dependent Mean	7.64167	Adj R-Sq	0.6339
Coeff Var	16.91501		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	12.26098	1.48804	8.24	<.0001
Tier4	1	-0.27806	0.06350	-4.38	0.0024
Tier2	1	0.09160	0.02863	3.20	0.0126

Possum 22

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	6	53.91718	8.98620	46.89	<.0001
Error	10	1.91645	0.19164		
Corrected Total	16	55.83363			

Root MSE	0.43777	R-Square	0.9657
Dependent Mean	7.61899	Adj R-Sq	0.9451
Coeff Var	5.74581		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	17.35570	1.64933	10.52	<.0001
Vines	1	-7.33684	0.57812	-12.69	<.0001
NEOPED	1	-1.02416	0.09836	-10.41	<.0001
NERVIL	1	-137.41312	37.92377	-3.62	0.0047
NOTMEN	1	0.10458	0.02208	4.74	0.0008
BLEDIS	1	-0.27332	0.07556	-3.62	0.0047
QUIACU	1	-0.14926	0.01548	-9.64	<.0001

Pooled models

Marh/May

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	10.39777	10.39777	6.99	0.0091
Error	148	220.26949	1.48831		
Corrected Total	149	230.66726			

Root MSE	1.21996	R-Square	0.0451
Dependent Mean	8.15777	Adj R-Sq	0.0386
Coeff Var	14.95460		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	8.02084	0.11228	71.44	<.0001
NEOPED	1	0.18926	0.07160	2.64	0.0091

July/September

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	5	38.43177	7.68635	3.63	0.0040
Error	139	294.14771	2.11617		
Corrected Total	144	332.57949			

Root MSE	1.45471	R-Square	0.1156
Dependent Mean	7.97693	Adj R-Sq	0.0837
Coeff Var	18.23642		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	7.77006	0.30498	25.48	<.0001
PSECRA	1	-0.92297	0.40511	-2.28	0.0242
PrefAUG	1	-0.02567	0.01107	-2.32	0.0218

SCHDIG	1	1.66339	0.67423	2.47	0.0148
QUIACU	1	0.04130	0.01908	2.17	0.0321
COPRHA	1	3.89858	1.43360	2.72	0.0074

November/January

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	5	46.67627	9.33525	5.09	0.0003
Error	109	199.85543	1.83354		
Corrected Total	114	246.53169			

Root MSE	1.35408	R-Square	0.1893
Dependent Mean	7.84161	Adj R-Sq	0.1521
Coeff Var	17.26790		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	8.01322	0.38950	20.57	<.0001
MEUAUS2	1	-0.79633	0.20833	-3.82	0.0002
NERVIL	1	17.35226	7.55588	2.30	0.0236
HerbGrass	1	0.67688	0.22692	2.98	0.0035
PRUVUL	1	90.53904	33.17169	2.73	0.0074
ELAHOO	1	-7.20337	3.56812	-2.02	0.0460

Annual

Analysis of Variance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	5	77.81558	15.56312	10.23	<.0001
Error	155	235.88035	1.52181		
Corrected Total	160	313.69593			

Root MSE	1.23362	R-Square	0.2481
Dependent Mean	8.21714	Adj R-Sq	0.2238
Coeff Var	15.01271		

Parameter Estimates

Variable	DF	Parameter Estimate	Standard Error	t Value	Pr > |t|
Intercept	1	8.68646	0.55034	15.78	<.0001
QUIACU	1	-0.06814	0.01468	-4.64	<.0001
COPROT	1	-0.44465	0.12282	-3.62	0.0004
NOTFUS	1	-0.01108	0.00437	-2.54	0.0122
RUBCIS	1	-1.12452	0.46952	-2.40	0.0178
SR	1	0.04678	0.02100	2.23	0.0273